

A Review of the Planthopper Genus *Nesodryas* Kirkaldy and Related Taxa (Homoptera: Fulgoroidea: Delphacidae)

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ABSTRACT. The genus *Nesodryas* Kirkaldy is redefined and confined to 2 endemic Hawaiian species, *N. freycinetiae* Kirkaldy from O'ahu and *N. swezeyi* Zimmerman from Hawai'i Island. *Marquedryas* n.gen. is established for 3 endemic species from the Marquesas Islands: *M. acamas* n.sp. and *M. laodice* n.sp. from Fatu Hivu I., and *M. oenone* (Fennah) n.comb. (referred from *Nesodryas*) from Hiva Oa I. *Nesodryas laocoon* Fennah from the Marquesas Islands (Hiva Oa I.) is referred to *Nesosydne* Kirkaldy. *Antidryas* n.gen. is erected for *A. antiope* (Fennah) n.comb. (referred from *Nesodryas*) from the southwestern Indian Ocean islands and southeastern Africa; the subspecies *N. antiope seychellensis* Fennah is synonymized with the nominate species. *Prasliniana* n.gen. is established monotypically for *P. pandanae* n.sp. from the Seychelles Islands. Phylogenetic relationships between these genera could not be assessed.

INTRODUCTION

A characteristic element in the fauna of many oceanic islands of the Pacific and the southwestern Indian Oceans is a group of planthoppers of the family Delphacidae that live on shrubs and trees rather than in low vegetation such as grasses, rushes, and sedges as they do elsewhere. These planthoppers are associated preferentially with Dicotyledones, but a few also with Monocotyledones (mostly palm trees and vines) and Pteridophyta. Morphologically, these delphacids have in common the shape of the post tibial spur (see e.g., Asche 1985) which is subulate, typically convex on both sides with distinct solid and cone-shaped teeth on the inner margin. Based on this character, Muir (1915) established for them a separate tribe within the subfamily Delphacinae, the Alohini. Muir's diagnostic concept was largely accepted. Subsequently, 200+ species were assigned to the Alohini, mainly by Muir (e.g., 1916, 1917, 1919, 1922) and Fennah (e.g., 1958). However, recent phylogenetic studies on Delphacidae based on various additional morphological characters including structures of the male and female genitalia have revealed a higher probability for the polyphyly of the Alohini than for their derivation from a common ancestral species (Asche 1985). According to this study, the configuration of the "alohine" post tibial spur is rather inconsistent in the Alohini. Moreover, it can be found similarly shaped in several other unrelated groups. Thus, the "alohine" spur is considered a weak character—even for diagnostic purposes. Today, the Alohini are regarded part of the tribe Delphacini, and within this tribe part of those taxa that display advanced oviduct glands (Asche 1985; for general morphology of oviduct glands see Strübing 1956a, b). The "alohine" genera are still very insufficiently investigated. Most are based on rather broad and inconsistent generic concepts and appear not to be monophyletic.

One of the smaller of these weakly defined "alohine" genera is *Nesodryas* Kirkaldy with 5 currently assigned species. Originally regarded as endemic to the Hawaiian Islands, this genus has since been recorded from the Marquesas Islands (Fennah 1958), from Mauritius and the Seychelles Islands (Fennah 1964), and from East Africa (Wilson 1987).

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Thus, *Nesodryas* appeared to be widely distributed. Fennah (1964) tried to explain this remarkable spot-like pattern of recent geographical distribution of *Nesodryas* species by the assumption that *Nesodryas* (and other "alohine" delphacids) might have radiated from a Pre-Glacial Antarctic continent. However, considerable morphological differences (especially in the male genital structures) of the Pacific and the Indian Ocean *Nesodryas* species do not support Fennah's assumption of a common ancestral stock for the species assigned to *Nesodryas*, but instead provide indications for their polyphyly. The following review attempts to redefine *Nesodryas* on a morphological and phylogenetic basis.

TAXONOMIC HISTORY

Nesodryas was established by Kirkaldy (1908) to accommodate a group of slender and delicate delphacid species from the Hawaiian Islands. Based on external appearance only, he separated *Nesodryas* from the genus *Nesothoe* Kirkaldy, assigning species with robust and stout body shape to the latter. As type species of *Nesodryas*, Kirkaldy designated *N. freycinetiae* Kirkaldy from O'ahu, which is associated with the native vine *Freycinetia arborea* (Pandanaceae).

Kirkaldy (1908) originally placed 5 species in *Nesodryas*: *N. freycinetiae*, *N. elaeocarpus*, *N. eugeniae*, *N. giffardi*, and later (1910) *N. dryope*. *Nesothoe* sensu Kirkaldy then contained 10 species. However, Muir (1916) modified Kirkaldy's generic concept by considering the differences between *Nesodryas* and *Nesothoe* as "only of sub-generic value", and sunk the latter as a subgenus of *Nesodryas*. Although Muir recognized the striking genital differences between the type species of *Nesodryas* and *Nesothoe*, he surprisingly regarded *Nesodryas freycinetiae* only as "an extreme form" (of the same genus) "either divergent or convergent", which was "not typical of the other species" (Muir 1916). Later, Muir described several more species in *Nesodryas* and *Nesodryas (Nesothoe)*, respectively. Muir's generic concept of *Nesodryas* went unchanged into the *General Catalogue of the Hemiptera* by Metcalf (1943). Only Zimmerman (1948) recognized the importance of the differences in the male and female genitalia between *Nesodryas* sensu stricto and *Nesothoe*. He redefined the 2 taxa on the basis of genital characters and, consequently, separated them as 2 different genera with uncertain phylogenetic relationships. He confined *Nesodryas* to a small genus of only 2 species, *N. freycinetiae* from O'ahu and *N. swezeyi* Zimmerman from Hawai'i Island, the latter feeding on the native palm *Pritchardia* (Arecaceae). *Nesothoe* then received the rest of the former *Nesodryas* species, i.e., the slender and delicate species, which—as Zimmerman realized—display a very similar configuration of the complex male genitalia as do the robust and stout forms.

Subsequently, 3 more species were placed in *Nesodryas*, 2 from outside Hawai'i, and 1 from outside the Pacific: 2 species from the Marquesas Islands, *N. oenone* Fennah (collected from *Pandanus* leaves) and *N. laocoon* Fennah (Fennah 1958); *N. antiope* Fennah from Mauritius, with the subspecies *N. antiope seychellensis* Fennah from the Seychelles Islands (Fennah 1964), both associated with coconut palms. *Nesodryas antiope* was also reported from Tanzania: Zanzibar, where it apparently causes damage to coconuts (Wilson 1987).

TAXONOMY

Nesodryas Kirkaldy

Nesodryas Kirkaldy, 1908: 203. Type species: *Nesodryas freycinetiae* Kirkaldy, 1908; by original designation.

Supplementary description. Additions and corrections to the genus definition of Zimmerman (1948) are as follows: macropterous, medium-sized, slender, and delicate delphacids with flattened appearance due to shallowly tectiformous tegmina. Coloration of body and legs in living individuals pale green, in dried museum specimens color fading to pale yellow or stramineous.

Head (Figs. 1–3, 16–18) including compound eyes ca. $2.5 \times$ wider than vertex at base, and $0.8 \times$ narrower than the pronotum. Vertex (Figs. 1, 4, 16, 19) rectangular with lateral margins slightly concave, anteriorly slightly produced, in midline ca. $1.2\text{--}1.3 \times$ longer than at base; compartments shallowly concave, covering nearly whole area of vertex, posterior compartments ca. twice as long as anterior one, median carina of posterior compartments faint; anterod of compartments at transition to frons a distinct transverse carina (Figs. 4, 19); angle of vertex to frons: ca. $70\text{--}75^\circ$. Frons (Fig. 3, 18) ca. $1.7\text{--}1.9 \times$ higher than wide (widest at level of ocelli), and ca. $1.7 \times$ higher than post and anteclypeus together; medially slightly elevated, lateral carinae slightly convex, median carina prominent; postclypeus with median carina faint, anteclypeus without carinae. Genae with oblique carina ridged, slightly curved (Figs. 2, 17). 1st antennal segment very short, ring-like, ca. $1.6 \times$ wider than long; 2nd antennal segment subcylindrical, widening to apex, ca. $5 \times$ longer than 1st; number and arrangement of sensory fields (= plaques) 16–7, i.e., 16 fields arranged in 7 longitudinal rows (for explanation see Asche 1985). Rostrum slightly surpassing mesotrochanters. Pronotum (Figs. 1, 16) rather flat with shallowly excavated posterior margin, ca. $0.7\text{--}0.8 \times$ shorter than vertex, carinae prominent, reaching posterior margin, lateral carinae straight or slightly convex, diverging; mesonotum (Figs. 1, 16) medially ca. $2.6\text{--}2.7 \times$ longer than pronotum, slightly vaulted, carinae straight, lateral carinae only slightly diverging. Tegmina (Figs. 6, 20) long, slender with rounded apex, ca. $3.8\text{--}3.9 \times$ longer than wide (widest shortly distad of nodal line), surpassing abdomen by about $1/2$ their length; claval vein and claval suture entering commissural margin at level of nodal line in an acute angle; hindwing with M and Cu distally fused; inner apical branch of Cu+M obsolete to apex. Hind legs (Fig. 5): post tibia ca. $1.42 \times$ longer than post tarsi together, single spine laterally at base, 5 (2+3) spines distally; 1st post tarsus ca. $2.3 \times$ longer than 2nd and 3rd together, ca. $1.8 \times$ longer than post tibial spur, distally with 5 (2+3) spines; 2nd post tarsus distally with 3 spines in a row; post tibial spur subulate, convex on both sides, with 4–5 well separated, cone-shaped teeth. Male drumming organ, as in many other Delphacini, with a well separated central plate in 2nd abdominal tergite and paired, elongate, filiformous apodemes of 2nd abdominal sternite erected dorsad.

Male genitalia. Figs. 7–13, 21–29. Genital segment (Figs. 7–9, 21–23) in caudal aspect elongate ovate, ca. $1.2 \times$ higher than wide; in lateral aspect irregularly trapezoidal, ventrally ca. $3.25 \times$ longer than dorsally, dorsal margin deeply excavated to receive the anal segment; in middle on each laterocaudal margin a long, spinose process directed caudad; at middle on ventrocaudal margin 2 long spinose processes forming a fork; diaphragm dorsally shallowly concave, without a central ornamentation. Anal segment (Figs. 10, 24, 26) moderately long, without any spinose processes, ventrocaudal corners slight-

ly lobe-like produced, distinctly beset with hairs; ventral side membranous; anal style simple, moderately long. Parameres (Figs. 10, 11, 24, 25) straight and slender, apically narrowing, together forming pincers. Aedeagus (Figs. 10, 12, 13, 24, 27–29) relatively short, tubular, slightly distad of its base almost evenly curved ventrad; phallotreme apicodorsally; shaft furnished with distinct, large tooth- or spine-like processes; basal part of aedeagus including chamber conspicuously contorted; suspensorium short, forming calyptra around aedeagal shaft; connective short, straight or slightly bent in middle.

Female genitalia. Figs. 14–15. Ovipositor sturdy, reaching posterior margin of anal segment; distal 1/2 median gonapophyses IX at dorsal margin with ca. 20–25 saw-like teeth; valvifers VIII slender, slightly widening at base; anal segment (Fig. 14) short, ring-like, flattened, caudal side almost entirely covered by anal style; anal style simple (not double as erroneously stated by Zimmerman 1948: 140, 157), strongly enlarged, ca. $2.2 \times$ longer than wide, and ca. $1.65 \times$ longer than width of anal segment, dorsally flattened with wrinkled surface, ventrally convex (Figs. 14 b, c).

Diagnosis. The genus *Nesodryas* can be characterized by the flattened shape of the body caused by shallowly tectiformous tegmina, by a comparatively large vertex with a distinct transverse carina at the transition of vertex to frons, by a medially projected frons with a single median carina, by the proportions of the antennal segments (1st segments extremely short, 2nd segment ca. $5 \times$ longer than 1st), by the partly fusion of M and Cu in the hind wing, by the spine configuration of the hind legs (post tibia laterally with 1 spine, 1st post tarsus with 5 (2+3) spines, 2nd post tarsus with 3 spines), and by the configuration of the male and female genitalia (e.g., male genital segment with a pair of long laterocaudal spinose processes and a pair of medioventral spines; anal segment devoid of spinose processes; female anal style strongly enlarged, covering nearly the entire caudal side of the anal segment, dorsally flat).

Geographical Distribution. Hawaiian Is: O'ahu, Hawai'i Island.

Remarks. The genus *Nesodryas* is here restricted to the generic concept of Zimmerman (1948) and includes only the 2 Hawaiian species *N. freycinetiae* and *N. swezeyi*. It can be distinguished by the diagnostic characters mentioned above, of which the following are considered apomorphic and thus constitute the genus: transverse carinae at transition to frons, reduction of the median lateral spine on the post tibia, fusion of M and Cu in the hind wing over a certain distance (a configuration that is similarly found in the delphacid tribe Tropidocephalini, but here independently evolved), laterocaudal margin of male genital segment each with a long spinose process and ventrocaudal margin medially with a pair of long spinose processes, anal segment elongate and devoid of spinose processes, and (possibly) the torsion of the aedeagal base; in the female genitalia the specifically shaped anal style. *Nesodryas* is well separated from all other Hawaiian delphacid genera by the unique combination of these characters. Currently, I cannot detect close relationships based on at least a single convincing synapomorphy neither to other Hawaiian taxa, nor to "alohine" Delphacini of the southeastern Pacific and Indian Oceans. An obvious similarity between the Hawaiian and non-Hawaiian *Nesodryas* is the presence of an enlarged anal style in the female genitalia. However, this character appears to be unsuitable in assessing close relationships between those taxa as it is quite differently shaped in

details (see below). In congruence with considerable differences in other genital characters, it seems likely that in each case an enlarged and superficially similar anal style has evolved independently. By these considerations, all non-Hawaiian species that have been assigned to *Nesodryas* can no longer be regarded congeneric, and consequently are transferred to other genera (see below).

The function of an enlarged female anal style is still unclear. It appears not to be a necessary functional response to the specific hostplants (palms) in regard to the digestion of certain plant saps, since the males do not possess a similarly modified and enlarged anal style. An enlarged female anal style could play a role during oviposition by producing wax to cover the eggs. Waxy exudations were found not only on the surface of the anal style but also on the ovipositor. The structure of the oviduct and its glands has not yet been examined.

The key to the 2 Hawaiian *Nesodryas* species as published by Zimmerman (1948: 158) is correct and needs no additions. For the species-discriminating characters see the corresponding diagnoses provided here.

Nesodryas freycinetiae Kirkaldy (Figs. 1–15)

Nesodryas freycinetiae Kirkaldy, 1908: 203.

Supplementary description. Body proportions and basic coloration largely as in Zimmerman (1948) and in the supplementary generic description. Body length (from apex of vertex to tip of tegmina): male 4.2–4.3 mm; female 4.5–4.6 mm. Coloration: vertex and pronotum each with 2 brown spots; tegmina hyaline, veins concolorous, 2 brown marks at commissural margin distad of nodal line and another opposite of these on outer margin along median curved vein arising from outer subapical cell.

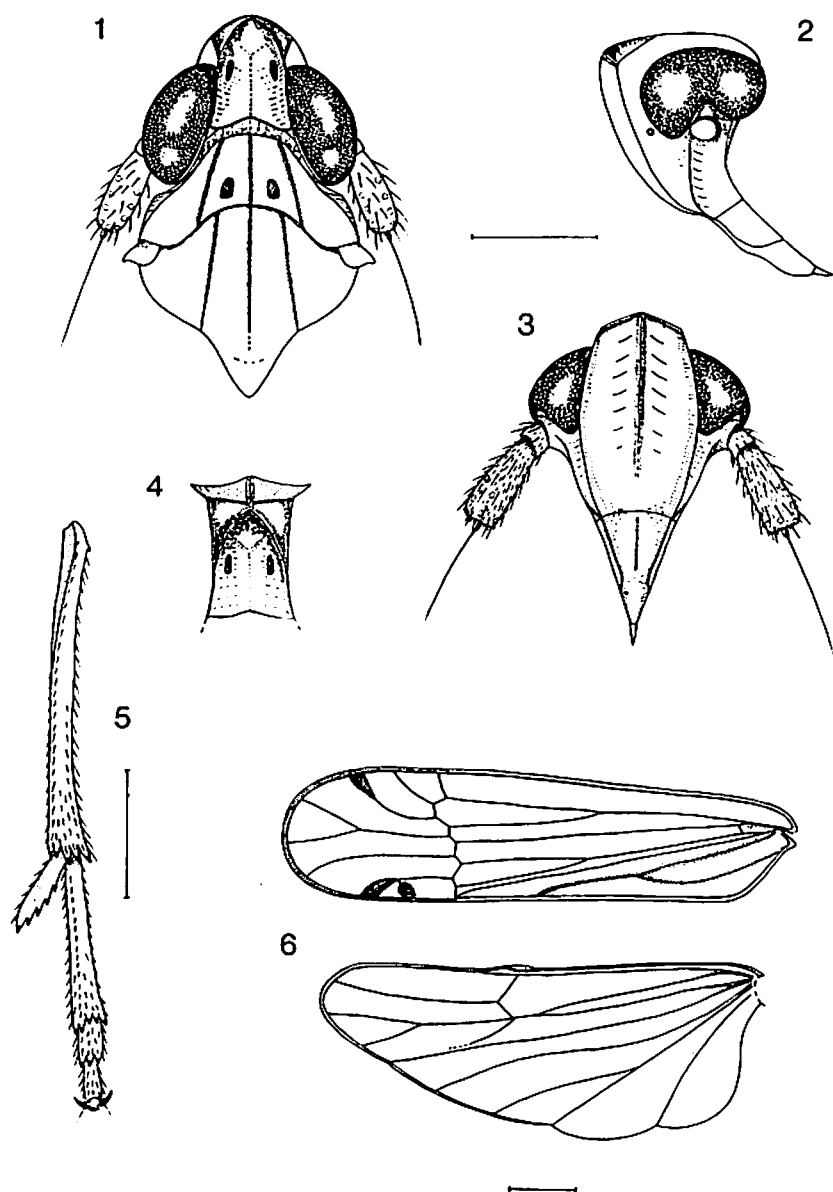
Male genitalia. Figs. 7–13. Genital segment (Figs. 7–9) in shape and proportions as defined for genus; laterocaudal spinose processes curved dorsad, at ventral margin furnished with row of 6–7 saw-like teeth; medioventral spinose processes distinctly diverging. Anal segment (Figs. 7, 10) as in generic description. Parameres (Figs. 7, 10, 11) continuously narrowing to finger-shaped apex directed mediad. Aedeagus (Figs. 10, 12, 13) strongly decurved ventrad; apex rounded; subapically on left side a row of 2–3 flat, apically rounded, plate-like processes; on right side at level of bending a single and subapical row of 3–4 of such flattened processes or teeth; suspensorium and connective as in generic description.

Female genitalia. Figs. 14, 15. As in generic description.

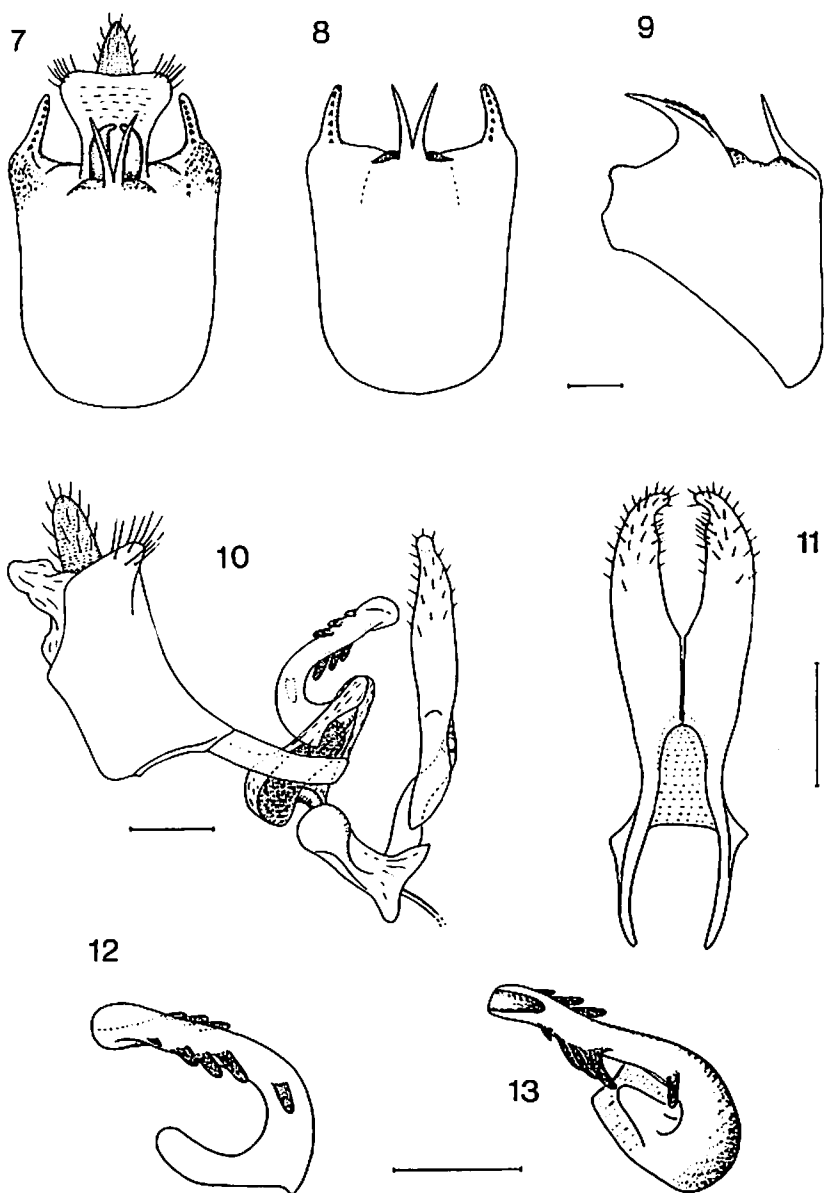
Diagnosis. *Nesodryas freycinetiae* can readily be distinguished from *N. swezeyi* by 4 conspicuous brown spots on the vertex and pronotum, by the largely uncolored tegmina without brown stripes, and by the shape of the male genitalia: laterocaudal spinose processes of the genital segment each with a row of teeth, the ventrally decurved aedeagus on both sides with a few flat, plate-like teeth.

Material examined. Holotype 2 from O'ahu, Honolulu, Pacific Heights Ridge, in BMNH. Paratype: 14, same data as holotype, BPBM.

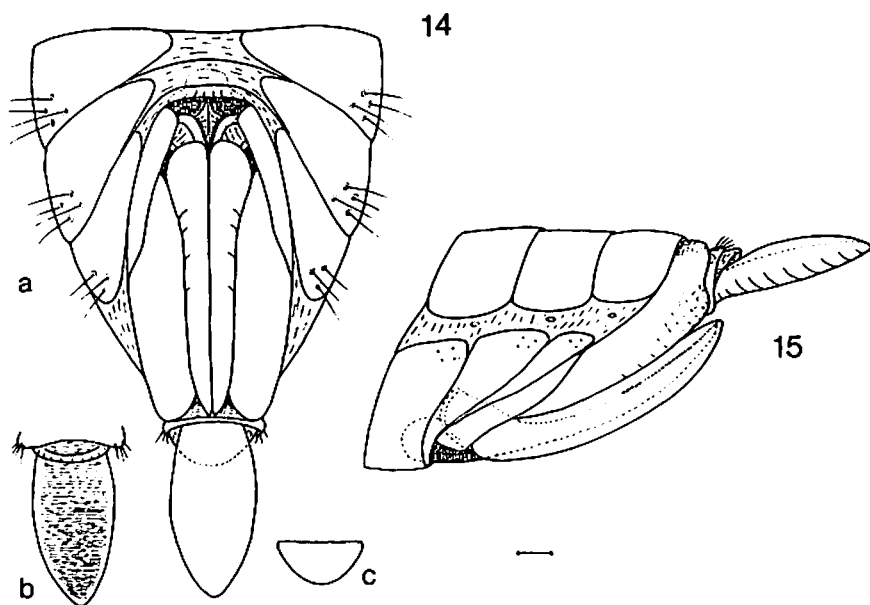
Non-type material. 14, 12, 1 nymph (5th instar), O'ahu, Mt. Tantalus, 1500 ft.



Figs. 1-6. *Nesodryas freycinetiae* Kirkaldy: 1-4, head, from O'ahu: Pacific Heights. 1, dorsal view with pro- and mesonotum; 2, left lateral view; 3, frontal view; 4, transition of vertex to frons; 5-6, from O'ahu: Mt. Tantalus; 5, left hind leg with post tibial spur, underside; 6, left tegmen and hind wing. Scales: 0.5 mm.



Figs. 7-13. *Nesodryas freycinetiae* Kirkaldy, male genitalia, specimen from O'ahu: Mt. Tantalus. 7, genitalia in repose, ventral view; 8, genital segment, ventral view; 9, same, left lateral view; 10, genitalia without genital segment, left lateral view; 11, parameres, ventral view; 12, aedeagus, right lateral view; 13, same, against 11 slightly twisted to right. Scales: 0.1 mm.



Figs. 14–15. *Nesodryas freycinetiae* Kirkaldy, female genitalia, specimen from O'ahu: Mt. Tantalus. 14 a, abdomen, ventral view; 14 b, anal style, dorsal view; 14 c, same, cross-section at middle; 15, tip of abdomen with anal style, ventral view. Scale: 0.5 mm.

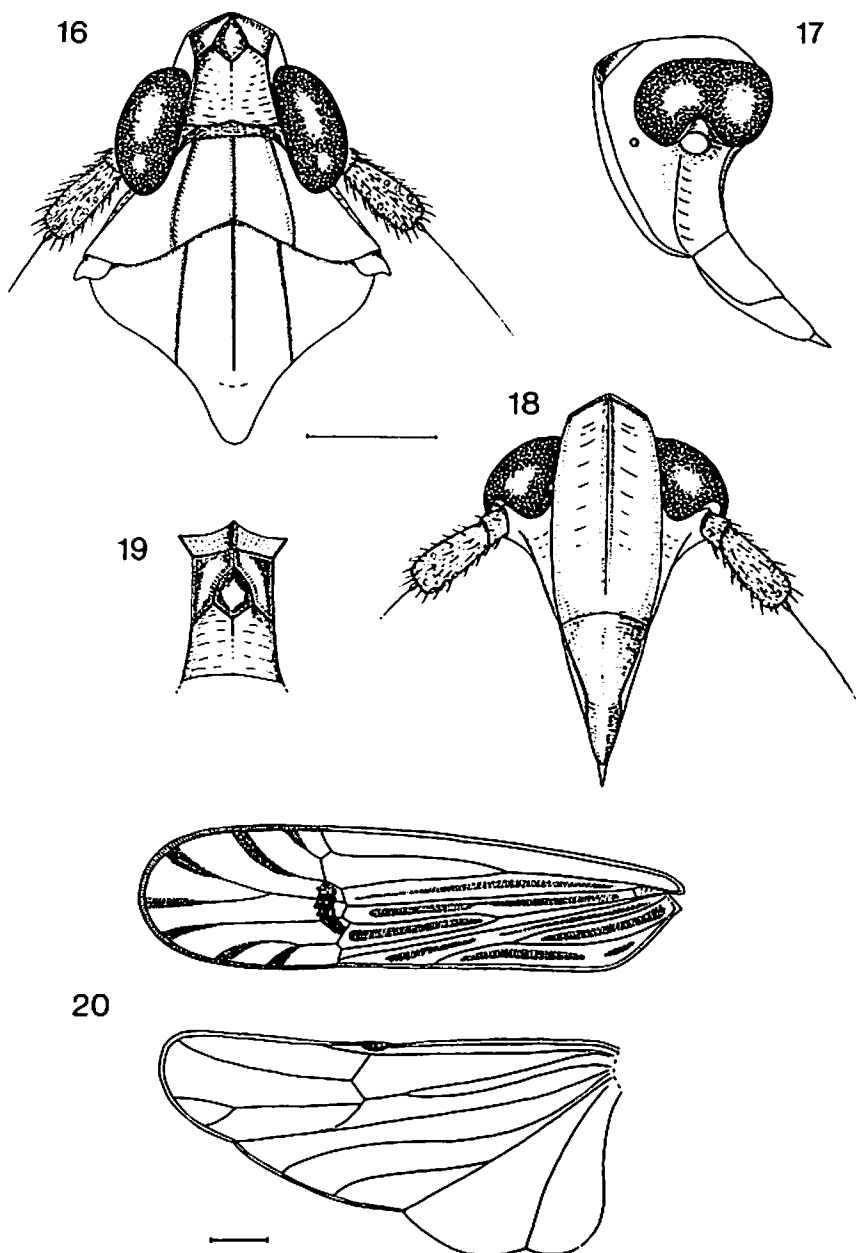
16.II.1916, W.M. Giffard (BPBM); 34, 22, *ibid.*, 16.X.1989, M. Asche & H. Hoch (AH).
Geographical Distribution. Hawaiian Is: O'ahu I. (e.g., Kirkaldy 1908; 1910; Swezey 1908, 1936; Muir 1916; Giffard 1917, 1922; Zimmerman 1948).

Host Plant. *Freycinetia arborea* (Pandanaceae) (e.g., Giffard 1917; Swezey 1908 (incl. life history data), 1936; Zimmerman 1948).

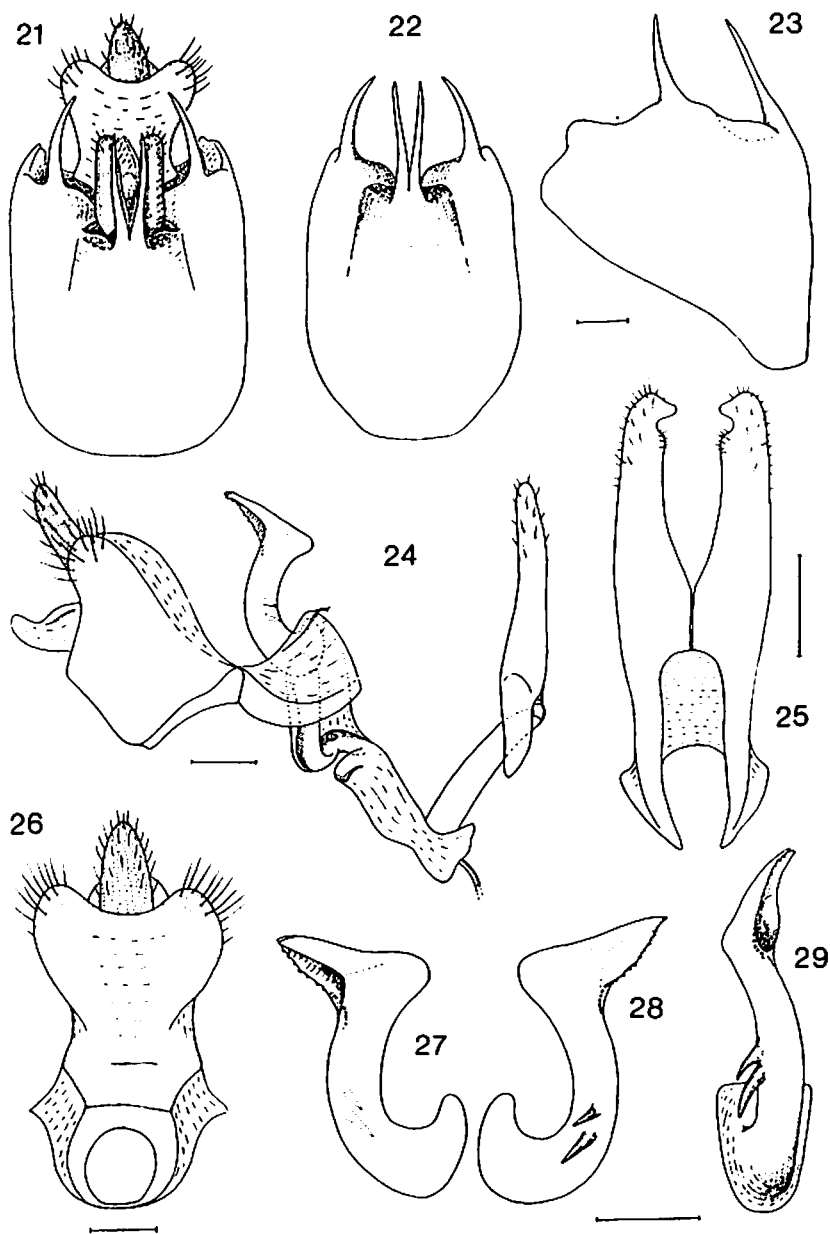
Nesodryas swezeyi Zimmerman (Figs. 16–29)

Nesodryas swezeyi Zimmerman, 1948: 159.

Supplementary description. Slightly larger and more robust in appearance than *N. freycinetiae*; body proportions and basic coloration as in Zimmerman (1948) in the supplementary generic description. Body length (from apex of vertex to tip of abdomen): male 4.5 mm, female 5.0 mm (not 6 mm as in Zimmerman 1948). Coloration: vertex and pronotum uniformly coloured without dark spots; tegmina basad of nodal line from R to commissural margin with longitudinal brown stripes between veins, at middle shortly distad of nodal line a short curved brown mark, apical veins to margin with dilute brown suffusion (Fig. 20).



Figs. 16–20. *Nesodryas swezeyi* Zimmerman, holotype from Hawai'i I. 16–19, head 16, dorsal view with pro- and mesonotum; 17, left lateral view; 18, frontal view; 19, transition of vertex to frons; 20, left tegmen and hind wing. Scales: 0.5 mm.



Figs. 21–29. *Nesodryas swezeyi* Zimmerman, male genitalia, holotype from Hawai'i I. 21, genitalia in repose, ventral view; 22, genital segment, ventral view; 23, same, left lateral view; 24, genitalia without genital segment, left lateral view; 25, parameres, ventral view; 26, anal segment, ventral view; 27, nodeagus, left lateral view; 28, same, right lateral view; 29, same, dorsal view. Scales: 0.1 mm.

Male genitalia. Figs. 21–29. Genital segment (Figs. 21–23) in shape and proportions as in generic description; laterocaudal spines almost straight, devoid of saw-like teeth on ventral margin; medioventral spines rather long, slender, less diverging than in *N. freycinetiae*. Anal segment (Figs. 21, 24, 36) as in generic description. Parameres (Figs. 21, 24, 25) at inner apical margin produced to small, pointed edge directed mediad. Aedeagus (Figs. 24, 27–29) with shaft almost evenly curved ventrad, apical part including the phallotreme in almost right angle bent dorsad, tapering to apex; phallotreme apically and exposed to left dorsal side; right margin of phallotreme flanked with row of ca. 18 minute teeth; right side of shaft shortly distad of its basal bending with 2 comparatively long spinose processes; suspensorium and connective as in generic description.

Female genitalia. As in generic description.

Diagnosis. *Nesodryas swezeyi* can be separated from *N. freycinetiae* by an unspotted vertex and pronotum, by the tegmina with brown longitudinal stripes, and by the male genitalia: laterocaudal spinose processes of the genital segment devoid of teeth, aedeagus apically recurved dorsad and apex pointed, a row of fine teeth around the phallotreme and 2 strong spine-like processes on right side of shaft (not flat, plate-like teeth).

Material examined. Holotype 4 (BPBM 1,827) and allotype 2, labelled "Hawai'i Island, Kulani Prison Rd., May 29, 1947, O.H. Swezey", collected from leaves of *Pritchardia* palm. Holotype and allotype in BPBM.

Geographical Distribution. Hawaiian Is: Hawai'i I. (Zimmerman 1948).

Host Plant. *Pritchardia* palm (Arecaceae) (Zimmerman 1948).

Remarks. On Hawai'i Island, *Pritchardia* (on Kulani Prison Road apparently *P. beccariana*) is the host plant of *Nesodryas swezeyi*, while in O'ahu another *Pritchardia* species is apparently the host plant of *Nesosydne gigantea* (Muir), one of the largest Hawaiian *Nesosydne* s.l. species (see Giffard 1922).

Marquedryas Asche, new subgenus

Type species. *Marquedryas laodice* n.sp.; here designated.

Description. Macropterous, medium-sized, slender, and delicate delphacids with steeply tectiformous tegmina and a distinctly, bulbous-like projected frons. Body length (from apex of frontoververtex to tip of tegmina): male 3.9–4.2 mm; female 4.4 mm. Ground color of body and legs pale yellow to stramineous; waxy exudations on tegmina and wings as well as in female genitalia; dark color patterns on head, thorax and tegmina (if present) of specific value (see below). Head (Figs. 30–32, 43–45, 58–60) ca. 2.5–2.7 × wider than vertex at base, ca. 0.8 × narrower than pronotum. Vertex and upper frons (frontoververtex) produced anterad in midline ca. 1.7–1.85 × longer than wide at base, posterior compartments of vertex large, in midline ca. 1.4–1.5 × longer than anterior one, compartments entirely on dorsal side, anterolateral carinae limiting compartments and median frontal carina distinctly prominent, together forming an inverted Y; angle between vertex and frons ca. 100°. Frons (Figs. 32, 45, 60) ca. 2.1–2.4 × higher than wide (widest at level of ocelli or slightly above frontoclypeal suture), ca. 1.6–1.7 × higher than post and anteclypeus

together; frontal area in upper part shallowly concave, ascending to simple, distinctly elevated median carina; frontal area in lower part above frontoclypeal suture strongly projected, forming nose-like bulb against postclypeus; surface of postclypeus shallowly convex, limited against anteclypeus by rather distinct notch, median carina prominent; anteclypeus cone-shaped, without carinae. Genae (Figs. 32, 44, 59) with oblique carina gently curving from lateral corner of frontoclypeal suture to lower anterior margin of antennal base. Ocelli small but distinct; compound eyes well developed, flat, kidney-shaped. 1st antennal segment cylindrical, short, ca. $1.4 \times$ longer than wide; 2nd antennal segment subcylindrical, widening to apex, ca. $2.3\text{--}2.5 \times$ longer than 1st; number and arrangement of sensory fields or placulae: 16-7 (see above, and Asche 1985). Rostrum attaining the mid of post trochanters. Pronotum medially ca. $0.55\text{--}0.65 \times$ shorter than frontovertex, disc narrow, almost plain, sides of pronotum steeply descending, posterior margin shallowly concave, carinae prominent, reaching posterior margin, lateral carinae almost straight or slightly convex, slightly diverging; mesonotum medially ca. $2.3\text{--}2.5 \times$ as long as pronotum, disc narrow, plain, carinae less prominent than in pronotum, lateral ones diverging and reaching posterior margin. Tegmina (Figs. 34, 47, 63) moderately long with broadly rounded apex, ca. $2.9\text{--}3.1 \times$ longer than wide (widest shortly distad of nodal line), surpassing tip of abdomen by about $1/3$ their length; clavus vein (A1) and claval suture distinct, distally entering nodal line at right angle, well separated from commissural margin; anterior branches of claval Y-vein (A2, A3) longer than common stalk that connects with commissural margin well before nodal line; commissural margin of clavus narrowly laminate; very fine granules along veins; in hind wings only slightly smaller than in tegmina, Cu and M including distal branches strongly developed. Hind legs (Fig. 62): post tibia ca. $1.3\text{--}1.4 \times$ longer than post tarsi together, laterally with 2, distally with 5 spines (almost in a row); 1st post tarsus ca. $1.8\text{--}2.1 \times$ longer than 2nd and 3rd together, ca. $1.8\text{--}2.0 \times$ longer than post tibial spur, distally with 6 (2+4) spines; 2nd post tarsus distally with 4 spines in a row; post tibial spur subulate, slender, with apical tooth distinct, inner margin with 5-9 well separated, cone-shaped teeth. Male drumming organ with paired elongate, filiform apodemes of 2nd abdominal sternite and well defined central plate in 2nd tergite as in other modern Delphacini.

Male genitalia. Figs. 35-42, 48-55, 64-68. Genital segment (Figs. 35-38, 48-51, 64-66) in caudal aspect elongate ovate, ca. $1.3 \times$ higher than wide; in lateral aspect trapezoidal, ventrally ca. $1.4 \times$ longer than dorsally, laterocaudal margins obliquely inflected mediad, both ventrocaudal corners at least slightly prominent if not projected into cone-shaped processes, medially at ventrocaudal margin a lobe- or fork-like protuberance; diaphragm covering the lower $1/2$ of caudal side, only slightly sunk cephalad against caudal margins, dorsal margin medially with distinct incision. Anal segment (Figs. 39, 52, 67) moderately long, ring-like; ventrocaudal margin projected caudad, closed by a sclerotized bridge; ventral side membranous; furnished either with long, paired spinose processes, or short, paired teeth. Parameres (Figs. 39-41, 52-54, 67, 68) comparatively long, distally narrowing to claw- or finger-like tip, together forming pincers. Aedeagus (Figs. 39, 42, 52, 55, 67) subtubular, at midlength of its shaft deflected ventrad, phallotreme slit-like, located subapically to apically at dorsocaudal margin; suspensorium forming short calyptra around aedeagal base; connective rather short, straight.

Female genitalia. Figs. 56-57. Ovipositor attaining middle of anal segment; slightly more than distal $1/2$ of median gonapophyses IX dorsally with row of 25-30 saw-like robust teeth; valvifers VIII broad at base, inner anterior margin of base with short edge;

anal segment short, ring-like, caudally truncate and shallowly concave; anal style enlarged, reversely spoon-like, strongly flattened, dorsal surface convex, ventral side concave (Figs. 56 a, b, 57).

Geographical Distribution. Marquesas Is.

Diagnosis. *Marquedryas* n.gen. can be distinguished from other "alohine" genera of the tribe Delphacini by the body shape with steeply tectiform, distally broadly rounded tegmina and a considerably bulbous-like projected frons as well as by the shape of the male and female genitalia. *Marquedryas* n.gen. differs from the Hawaiian genus *Nesodryas* by the habitus (compressed instead of flattened appearance), the proportions and carination of the head (vertex at transition to frons without transverse carinae), by the 1st antennal segment distinctly longer than wide (instead of shorter than wide), by the possession of 2 lateral spines on the post tibia (instead of 1), by the right-angulate entry of the claval vein and suture into the nodal line well distant of the commissural margin (instead of an acute-angulate entry at the commissural margin); by the venation of the hindwing with Cu and M separated over the whole distance (not partly fused), and by the following genital characters: in the male genitalia latero- and ventrocaudal margins of genital segment without spinose processes but with projected ventrocaudal corners instead, and with laterocaudal margin obliquely inflected; dorsal margin of diaphragm medially incised instead of being continuous; anal segment with paired tooth-like or spinose processes instead of being devoid of any processes; anal style of females strongly flattened with dorsal surface convex, ventrally concave.

Remarks. The following characters are interpreted as apomorphic, and distinguish the genus *Marquedryas*: a bulb-like projected frons; special venation of tegmina, especially the position of the claval vein and suture; genital characters: shape of the male genital segment with an obliquely inflected laterocaudal margin, the configuration of the ventrocaudal margin, the shape of the diaphragm with its mediiodorsal incision, and the distinctly flattened anal style of the female genitalia. The phylogenetic relationships of *Marquedryas* with other "alohine" genera of the Pacific and other regions are difficult to judge. The apparently monophyletic Hawaiian genus *Nesodryas* resembles *Marquedryas* in the shape of the female genitalia by the possession of an enlarged anal style. However, considering the morphological differences of this structure in addition to other dissimilarities in both groups, this character is regarded as homoplastic (see the above remarks on *Nesodryas*). As no close relationships based on synapomorphies to either the Hawaiian taxa or to other Delphacini could be found, *Marquedryas* apparently represents a separate and rather isolated evolutionary line.

KEY TO SPECIES OF *MARQUEDRYAS*, NEW GENUS

1. Tegmina from base to apex with a broad, dark brown longitudinal stripe (Fig. 34 a), sides of pro- and mesonotum, lower frons and genae dark brown (Figs. 30–32) *Marquedryas acamas*, n.sp.
- Tegmina without a dark longitudinal stripe, head without dark coloration 2
- 2(1). Tegmina at entry of common stalk of claval Y-vein into commissural margin with a distinct oblique mark, apical margin fringed by a diffusely yellow-brown band, nodal line brown in middle (Fig. 47); lower frons very strongly produced (Fig. 44); in male

- genitalia, anal segment with long paired spinose processes (Fig. 52), genital segment with caudoventral corners distinctly produced (Figs. 50, 51), aedeagus on each side of distal half with a row of teeth *Marquedryas laodice*, n.sp.
- . Tegmina at entry of claval Y-veins into commissural margin with a small, linear mark, nodal line in middle concolorous, only marginally brown, apical margin not fringed by a yellow-brown band (Fig. 63); lower frons less strongly produced (Fig. 59); in male genitalia anal segment with only minute paired tooth-like processes (Fig. 64, 67), genital segment with ventrocaudal corners only slightly produced (Figs. 65, 66), aedeagus without teeth *Marquedryas oenone* (Fennah)

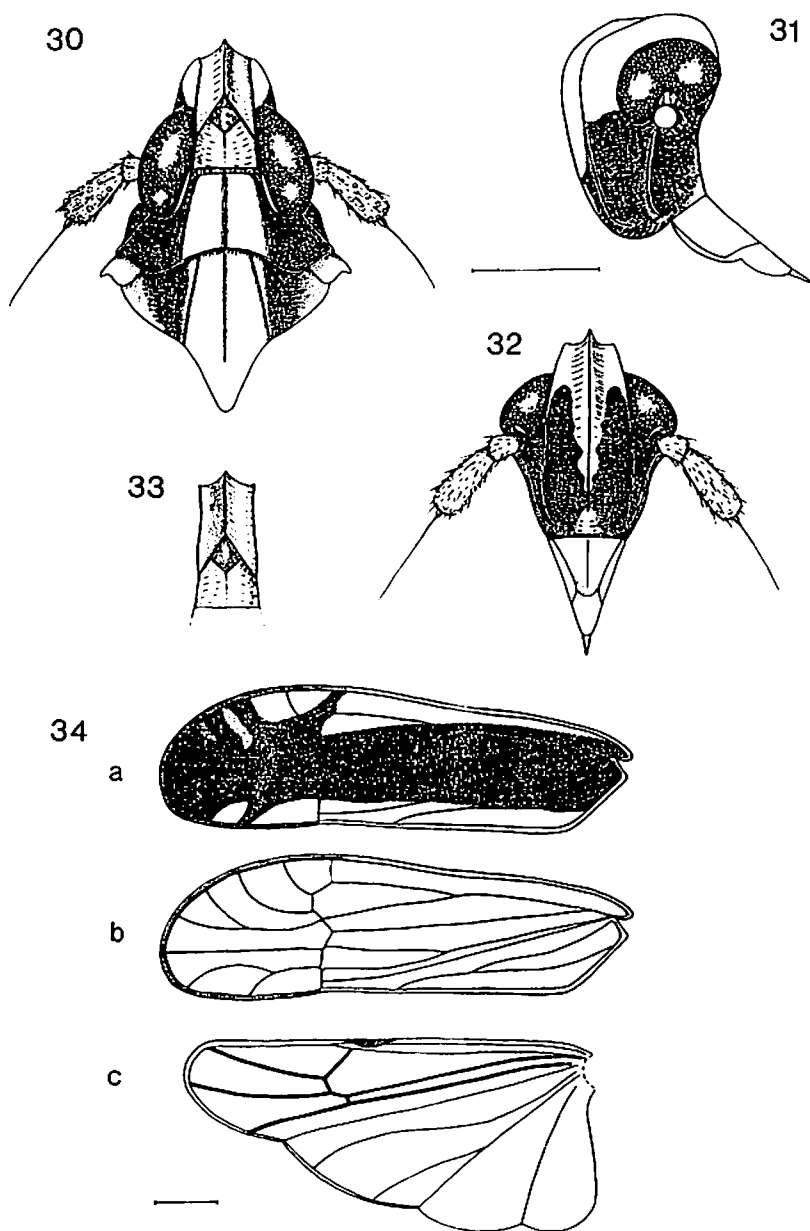
***Marquedryas acamas* Ashe, new species (Figs. 30–42)**

Description. In habitus and color patterns almost resembling species of the genus *Sardia* Melichar. Body length (from apex of frontovertex to tip of tegmina): 3.9 mm. Coloration: ground color of body and legs pale yellow; lower 2/3 of frons except a small stripe along median carina and lateral parts of head from level of ocelli to frontoclypeal suture contrasted dark brown (Figs. 31, 32); lateral portions of pro- and mesonotum dark brown (Fig. 30); tegmina and wings slightly opaque; tegmina with broad dark brown longitudinal band from base to apex enclosing claval veins A2, A3, inner subapical cell (outer subapical cell uncolored), Cu, M, and R; apex distad of nodal line almost entirely brown, for pattern see Fig. 34a; hind wings with Sc+R, M, and Cu incl. distal branches brown, otherwise concolorous; tegulae pale yellow; abdomen whitish to pale yellow, genitalia honey yellow. Vertex and upper frons (Fig. 30, 33) considerably produced anterad, in dorsal aspect medially ca. 1.85 × longer than wide at base. Frons (Fig. 32) ca. 2.4 × higher than wide (widest slightly above frontoclypeal suture), in lower part bulb-like projection strongly developed (Fig. 31). 2nd antennal segment ca. 2.3 × longer than 1st. Other characters of head and thorax as in generic description. Tegmina (Fig. 34 a, b) ca. 3.1 × longer than wide; venation see Fig. 34 b. 1st post tarsus ca. 2.1 × longer than 2nd and 3rd together, ca. 1.8 × longer than post tibial spur, with 5 cone-shaped teeth on inner margin.

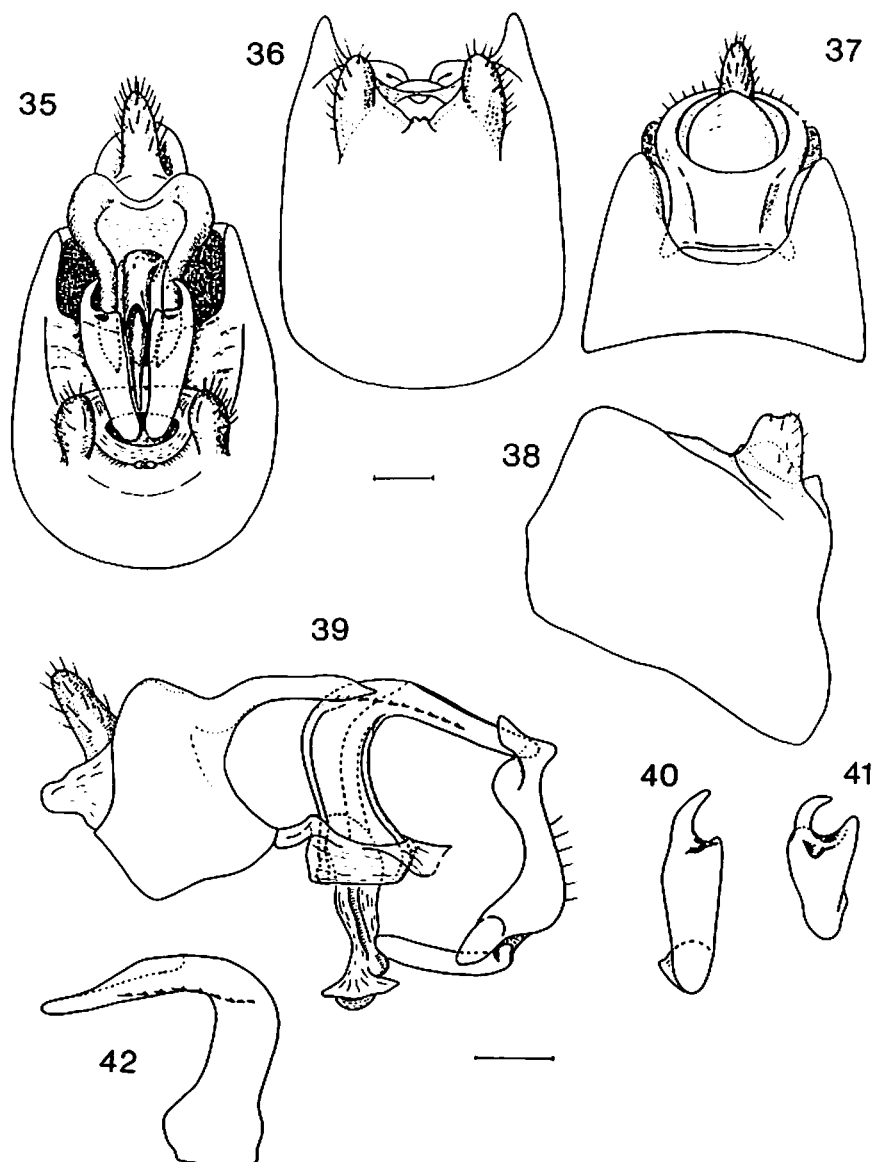
Male genitalia. Figs. 35–42. Genital segment (Figs. 35–38) with ventrolateral corners on each side produced into distinct cone-shaped process that is apically slightly notched (Figs. 37, 38); ventrocaudal margin between these cone-shaped processes medially with short subtriangular, apically slightly incised protuberance (Fig. 36). Anal segment (Figs. 35, 37, 39) with lateroventral processes long, slightly sinuate, slightly compressed, apically pointed. Parameres (Figs. 39–41) in lateral aspect sinuate, subapically slightly dilated, narrowing and forming short edge directed mediodorsad, another short lobe directed ventrad, and slender, claw-like tip directed mediodorsad. Aedeagus (Figs. 39, 42) with shaft in basal 1/2 robust, cylindrical, then narrowing to apex, distad of phallosome compressed; in decurved distal part on left side a longitudinal row of 10 teeth leading to level of phallosome, on right side a row of 9 teeth almost parallel to left one; suspensorium and connective as in generic description.

Females. Unknown.

Diagnosis. *Marquedryas acamas* n.sp. can readily be separated from the other 2 congeners by its dark brown coloration of the lower parts of frons and genae, and by the color pattern of the tegmina with a broad longitudinal band from base to apex. In the male gen-



Figs. 30-34. *Marquedryas acamas* Asche, n.sp., holotype from Fatu Hiva I. 30-33, head; 30, dorsal view with pro- and mesonotum; 31, left lateral view; 32, frontal view; 33, transition of vertex to frons; 34, left tegmen and hind wing; a, color pattern of tegmen; b, venation of tegmen; c, hindwing. Scales: 0.5 mm.



Figs. 35–42. *Marquedryas acamas* Asche, n.sp., male genitalia, holotype from Fatu Hiva I. 35, genitalia in repose, ventrocaudal view; 36, genital segment, caudal view; 37, same, dorsal view; 38, same, left lateral view; 39, genitalia without genital segment, left lateral view; 40, left paramere, ventral view; 41, same, view on the tip; 42, aedeagus, right lateral view. Scales: 0.1 mm.

italia it is distinguished from *M. oenone* (see below) by the shape of the genital segment, the anal segment, and the aedeagus. From *M. laodice* n.sp. (see below) it differs by the dentation of the aedeagus and by the less prominent medioventral process.

Type data. Holotype 4 (BPBM 15,318), MARQUESAS IS: FATU HIVU I., Namana Ridge, 650–800 m, 1.VIII.1977, on *Piper* sp., W.C. Gagné. Holotype in BPBM.

Geographical Distribution. Marquesas Is.: Fatu Hiva I.

Host Plant. *Piper* sp. (Piperaceae).

Remarks. *Marquedryas acamas* n.sp. resembles *M. laodice* n.sp. (see below) in the configuration of the male genitalia, and is probably more closely related to this species than to *M. oenone* (see also remarks under *M. laodice*).

Marquedryas laodice Asche, new species (Figs. 43–57)

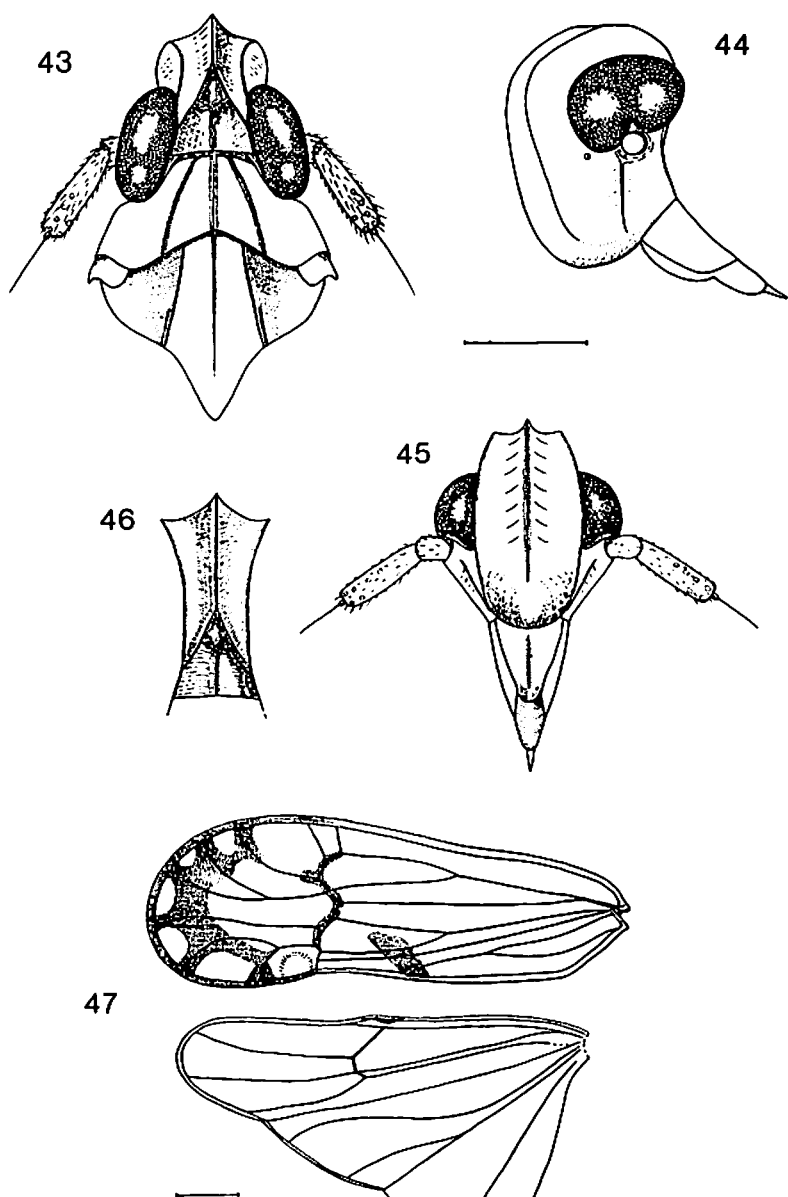
Description. Body length (from apex of frontovertex to tip of tegmina): male 4.0–4.2 mm (4.1 ± 0.05 mm; $n = 8$); female 4.4 mm ($n = 2$). Coloration: body and legs nearly uniformly whitish to pale yellow, lateral carinae of pronotum, in some individuals lateral parts of mesonotum and frontal bulb light brownish; tegmina opaque, powdered white, on inner margin at entry of common stalk of Y-shaped claval veins a short, oblique, linear brown mark, nodal line and apical veins near margin yellowish brown to fuscous, subapically along margin a dilute yellow to light brown suffusion (Fig. 47), veins concolorous, hairs whitish; hind wings strongly powdered white, veins concolorous except for brownish cross veins; male genital structures generally honey yellow; cone-shaped projections of genital segment dark brown; in female genitalia ovipositor and anal style diffusely light brown.

Vertex and upper frons (Figs. 43, 46) in midline ca. $1.8 \times$ longer than vertex at base, lateral margins slightly concave. Frons (Fig. 45) ca. $2 \times$ as high as wide (widest shortly above level of ocelli); frontal bulb above frontoclypeal suture very strongly pronounced (Fig. 44); 2nd antennal segment ca. $2.5 \times$ longer than 1st. Other characters of head and thorax as in generic description. Tegmina ca. $2.9 \times$ longer than wide, venation as in Fig. 47. 1st post tarsal segment ca. $2.5 \times$ as long as 2nd and 3rd together, ca. $1.9 \times$ longer than post tibial spur; post tibial spur with 8–9 cone-shaped teeth on inner margin.

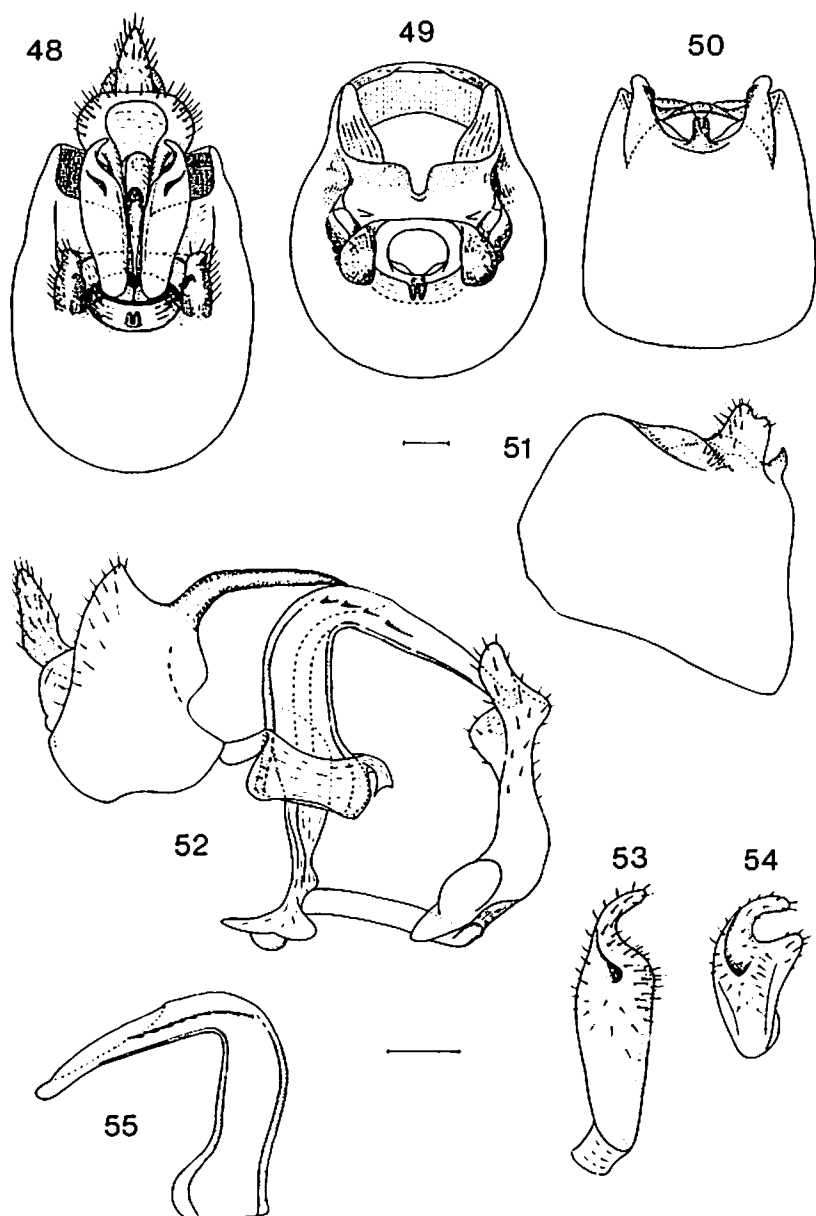
Male genitalia. Figs. 48–55. Generally similar to configuration in *M. acamas* n.sp. Genital segment (Figs. 48–51) with paired ventrolateral cone-shaped projections elongate, apically bilobate, between these projections at center of ventrocaudal margin a short, slender, apically distinctly forked protuberance. Anal segment (Figs. 48, 52) similar to that in *M. acamas* n.sp., lateroventral margins produced into long, apically pointed spinose process slightly bent ventrad. Parameres (Figs. 48, 52–54) in lateral aspect slightly curved dorsad, dilating to subapical region, forming an inner lobe directed mediodorsad, short ventral lobe, and longer, slender, finger-shaped process slightly inflected mediad. Aedeagus (Figs. 52, 55) similar to that in *M. acamas* n.sp., in decurved distal 1/2 on left side a short row of 4 teeth, on right side a parallel yet longer row of 8–9 teeth.

Female genitalia. Figs. 56–57. As in generic description.

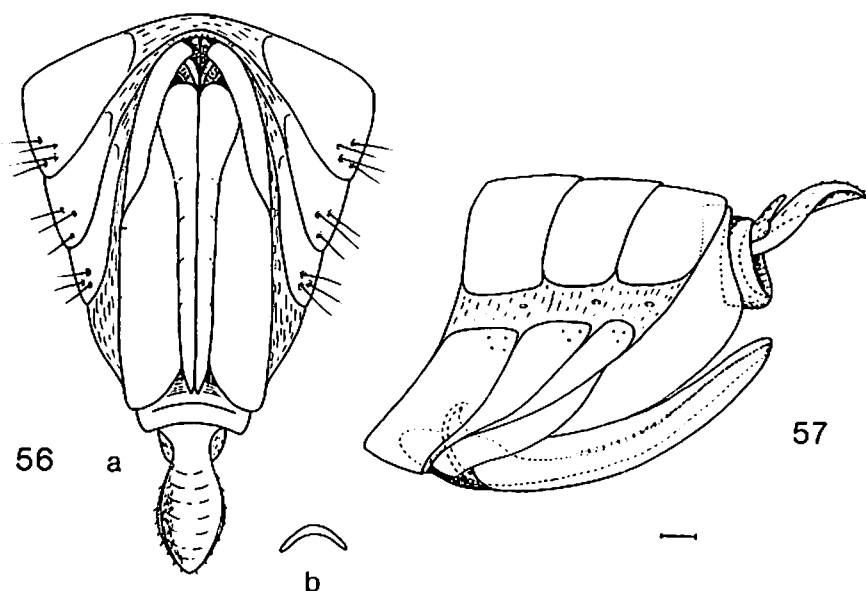
Diagnosis. *Marquedryas laodice* n.sp. can be distinguished from the other 2 congeners by



Figs. 43–47. *Marquedryas laodice* Asche, n.sp., paratype from Fatu Hiva I. 43–46, head; 43, dorsal view with pro- and mesonotum; 44, left lateral view; 45, frontal view; 46, transition of vertex to frons; 47, left tegmen and hind wing. Scales: 0.5 mm.



Figs. 48-55. *Marquedryas laodice* Asche, n.sp., male genitalia, paratype from Fatu Hiva I. 48, genitalia in repose, ventrocaudal view; 49, genital segment, caudal view; 50, same, ventral view; 51, same, left lateral view; 52, genitalia without genital segment, left lateral view; 53, left paramere, ventral view; 54, same, view on the tip; 55, aedeagus, right lateral view. Scales: 0.1 mm.



Figs. 56-57. *Marquedryas laodice* Asche, n.sp., female genitalia, paratype from Fatu Hiva I. 56a, abdomen, ventral view; 56b, anal style, cross-section in middle; 57, tip of abdomen with anal style, ventral view. Scale: 0.5 mm.

the strongly pronounced frontal bulb (strongest within the genus), by the color pattern of the tegmina with a fringe-like suffusion along the apical margin, and by the structures of the male genitalia. It differs from *M. oenone* mainly by the ornamentation of the ventro-caudal margin, by the possession of long paired spinose processes of the anal segment (instead of short paired teeth), and by a dentated aedeagus (instead of an aedeagus devoid of teeth). In the configuration of the male genitalia it resembles *M. acamas*, but differs in details, especially in the shape of the medioventral process and in the number and arrangement of aedeagal teeth.

Material examined. Holotype 4 (BPBM 15,319), MARQUESAS IS: FATU HIVA I.: Puna 'ita'i Ridge, above Omoa, 850 m, Coleman lamp, 23.VII.1988, S.L. Montgomery, Fatu Hiva Biol. Exped. Holotype in BPBM. Paratypes: 64, 22, same data as holotype; 24, same data as holotype except for 21.VII.1988, at MV light. Paratypes in BPBM.

Geographical Distribution. Marquesas Is: Fatu Hiva I.

Host Plant. Unknown.

Remarks. *Marquedryas laodice* n.sp. shares with *M. acamas* n.sp. the general shape of the male genitalia. However, the structures of the male genitalia are difficult to evaluate for assessing phylogenetic relationships within the genus. It is conceivable that the strong-

ly pronounced and apically notched ventrocaudal corners, the medioventral process with apical incision, and perhaps the configuration of the subapical part of the parameres with a short ventral lobe, a longer median lobe, and a claw-like tip represent apomorphic characters that, in this particular display and combination, are only present in these 2 species but not in *M. oenone*, thus *M. laodice* and *M. acamas* may be regarded as sister species. Other genitalic characters such as a dentated aedeagus and an anal segment with long paired spinose processes represent most likely a plesiomorphic state (see remarks under *M. oenone*).

***Marquedryas oenone* (Fennah), new combination (Figs. 58–68)**

Nesodryas oenone Fennah, 1958: 190.

Supplementary Description. A few additions and corrections to the original description (Fennah 1958) are as follows: Body length: male 4.2 mm; female 4.4 mm. Frontovertex (Figs. 58, 61) in midline ca. $1.7 \times$ (not $2 \times$) longer than vertex at base. Frontal bulb above frontoclypeal suture distinct but slightly less projected as in *Marquedryas acamas* and *M. laodice*. Venation of tegmen and hind wing as in Fig. 63. Hindleg (Fig. 62): 1st post tarsus ca. $1.8 \times$ longer than 2nd and 3rd together, and ca. twice as long as post tibial spur; post tibial spur (Fig. 62) with 6–8 teeth on inner margin (in some individuals varying on left and right side). Other body characters as in generic description.

Male genitalia. Figs. 64–68. Genital segment (Figs. 64–66) with ventrocaudal corners only slightly produced, not distinctly cone-shaped, apically notched, medioventral projection tongue-like. Anal segment (Figs. 64, 67) devoid of long, paired, spinose processes, but each ventrocaudal corner with very short, acute tooth-like process. Parameres (Figs. 67, 68) double S-shaped, continuously tapering (without subapically dilated area) tips slender, converging. Aedeagus (Fig. 67) devoid of teeth.

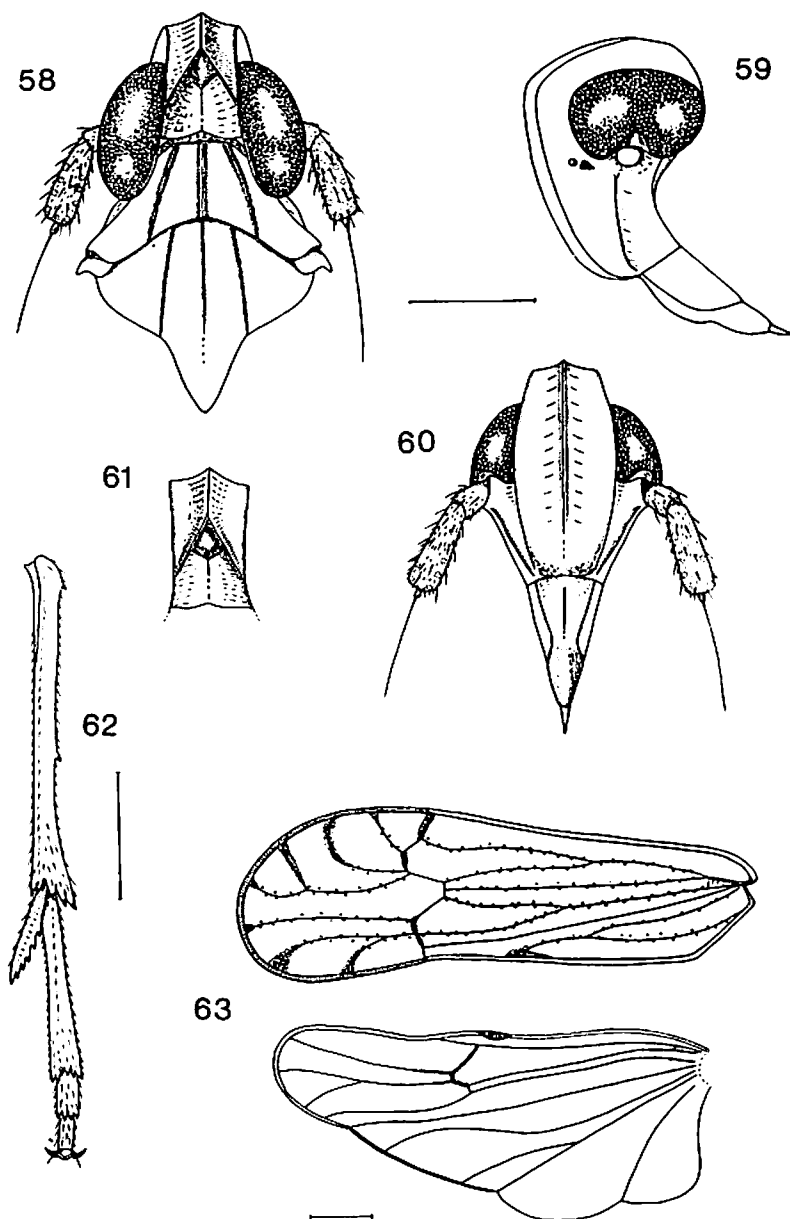
Female genitalia. As in generic description.

Diagnosis. *Marquedryas oenone* can be distinguished from *M. acamas* and *M. laodice* mainly by the less pronounced frontal bulb above the frontoclypeal suture and by the following structures of the male genitalia: genital segment with ventrocaudal corners only slightly produced (not distinctly cone-shaped projected), medioventral process tongue-shaped without apical incision, anal segment with short tooth-like paired processes (instead of long spinose processes), parameres evenly tapering to apex without a subapical dilation, aedeagus devoid of teeth.

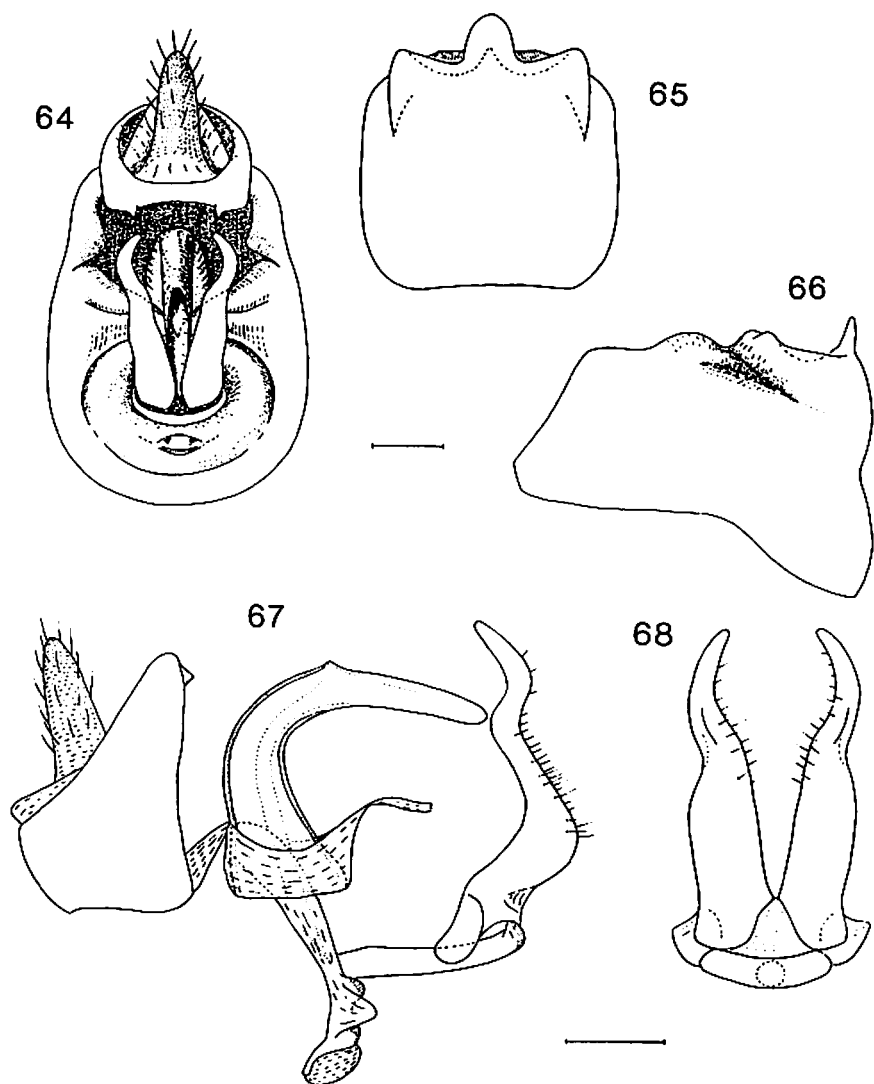
Material examined. Holotype 4 (BPBM 2,679) MARQUESAS IS: HIVA OAI., Kaava Ridge, 2800 ft. 7.I.1932, on leaves of *Pandanus*, Le Bronnec, Pacific Entomological Survey. Holotype in BPBM. Paratypes: 12, same locality data as holotype, on *Pandanus*; 14, same locality, 27. X.1937, beating on *Ageratum conyzoides*, Le Bronnec, Pacific Entomological Survey. Paratypes in BPBM.

Geographical Distribution. Marquesas Is: Hiva Oa I. (Fennah 1958: 191).

Host Plants. *Pandanus* (Pandanaceae) (see Fennah 1958). *Ageratum conyzoides* (Asteraceae) as indicated on the label of a paratype male (? accidental).



Figs. 58–63. *Marquedryas oenone* (Fennah): 58–61, head, holotype from Hiva Oa I. 58, dorsal view with pro- and mesonotum; 59, left lateral view; 60, frontal view; 61, transition of vertex to frons; 62–63, paratype from Hiva Oa I.: 62, left hind leg with post tibial spur, underside; 63, left tegmen and hind wing. Scales: 0.5 mm.



Figs. 64–68. *Marquedryas oenone* (Fennah), male genitalia, paratype from Hiva Oa I. 64, genitalia in repose, ventrocaudal view; 65, genital segment, ventral view; 66, same, left lateral view; 67, genitalia without genital segment, left lateral view; 68, parameres, ventral view. Scales: 0.1 mm.

Remarks. Within the genus, *Marquedryas oenone* represents a species outside of a potential sister group of *M. acamas* and *M. laodice*, since it does not share the apparently apomorphic characters such as the strongly pronounced ventrocaudal corners and the apically incised medioventral process of the male genital segment, and the subapically dilated parameres. The configuration of these characters in *M. oenone* seems to represent a plesiomorphic state. The unarmed aedeagus and the short teeth-like paired processes of the anal segment are probably oligomerized apomorphies, and could thus be regarded as autapomorphies of *M. oenone*.

Nesosydne laocoon (Fennah), new combination

Nesodryas laocoon Fennah, 1958: 191.

Due to incongruences in external characters as well as in male genital structures, *Nesodryas laocoon* Fennah from the Marquesas Is: Hiva Oa I. (Fennah 1958) is no longer regarded as a species of *Nesodryas*. Equally, it cannot be placed in *Marquedryas* n. gen. Provisionally, this species is here referred to the genus *Nesosydne* Kirkaldy.

Remarks. The Marquesas Island species assigned to *Nesosydne* (see Fennah 1958) reflect a very preliminary systematic status. An evaluation of this problematic assessment will be attempted in another paper.

Antidryas Asche, new genus

Type species. *Nesodryas antiopae* Fennah, 1964; here designated.

Description. Macropterous, small to medium-sized Delphacidae with a slender and delicate appearance. Coloration of body and legs whitish yellow to pale stramineous. Head (Figs. 69–71) ca. 2.4–2.5 × wider than vertex at base, ca. 0.8 × narrower than pronotum. Vertex (Figs. 69, 72) nearly rectangular with lateral margins slightly concave, compartments entirely on dorsal side, covering most of vertex, anterior compartment elongate, projected anterad, ca. as long or slightly longer than posterior compartments, latter without distinct median carina, shallowly concave; angle of vertex to frons ca. 80–85°, transition in profile rounded. Frons (Fig. 71) ca. 1.8–1.9 × higher than wide (widest shortly below level of ocelli), ca. 1.4 × higher than post and anteclypeus together; lateral margins shallowly concave, median carina simple, prominent, frontal area shallowly concave, ascending to median carina; postclypeus convex with median carina distinct, anteclypeus rounded without carinae. Genae (Fig. 70) with oblique carina sharp-edged; ocelli present; compound eyes well developed. Antennal segments cylindrical, 1st segment ca. 1.6–1.7 × longer than wide (not 1.2:1 as indicated in Fennah (1958) for *N. antiopae*); 2nd segment ca. 2.4–2.5 × longer than 1st; number and arrangement of antennal sensory fields: 16-7. Rostrum attaining the anterior margin of post trochanters. Pronotum (Fig. 69) with area of disc plain, in midline ca. 0.6–0.7 × shorter than vertex, posteriorly shallowly concave, carinae prominent, reaching posterior margin, lateral carinae diverging, straight or slightly convex; mesonotum (Fig. 69) in midline ca. 2.7–2.8 × longer than pronotum, carinae distinct, approximate, lateral carinae nearly straight, only slightly diverging. Tegmina (Fig. 74) slender with evenly rounded apex, ca. 3.4–3.5 × longer than wide (widest distad of nodal line), surpassing tip of abdomen by slightly more than 1/3 their length; outer sub-

apical cell considerably larger than inner one; hind wings with M and Cu close and parallel to each other. Hind legs (Fig. 73): post tibia ca. $1.4 \times$ longer than post tarsi together, laterally with 2, distally with 5 (2+3) spines; 1st post tarsus ca. $1.9\text{--}2.0 \times$ longer than 2nd and 3rd post tarsi together, ca. $2 \times$ as long as post tibial spur, distally with 6 (2+4) spines; 2nd post tarsus segment distally with 3-4 spines in a row; post tibial spur slender, solid, with inner area opposite to 1st post tarsus segment shallowly concave, subtriangular in cross-section (not with both sides convex), inner margin with 4-12 small but solid teeth. Male drumming organ with separated dorsal plate in center of 2nd abdominal tergite, and with long, paired, filiformous apodemes of 2nd abdominal sternite erected dorsad as in other Delphacini.

Male genitalia. Figs. 75-85. Genital segment (Figs. 75-77) in caudal aspect as high as wide or slightly higher, laterodorsal corners distinctly produced; ventrally ca. $3 \times$ longer than dorsally, dorsal margin deeply excavated to receive entirely the anal segment; ventrocaudal margin shallowly concave, devoid of processes; diaphragm dorsally deeply emarginated, centrally roof-like projected caudodorsad; opening for parameres flat, ovate. Anal segment (Fig. 78) short, ring-like, ventrally membranous, ventrolateral margins inflected medioventrad, produced into paired spinose processes. Parameres (Figs. 78, 81-85) moderately long, stout, at base with short lobe-like process directed mediocaudad; in caudal aspect diverging at base, slightly converging at apex, apically slightly dilated, truncate with outer and inner corners produced. Aedeagus (Figs. 78-80) short, tubular, nearly straight, with compressed and longitudinally furrowed dilation at shaft base; phallosotreme apically; suspensorium short, ring-like, embracing base of aedeagal shaft; connective short, slightly bent at middle.

Female genitalia. Figs. 86, 87. Ovipositor sturdy, reaching the posterior margin of the anal segment; distal 1/2 of median gonapophyses IX at dorsal margin with 35-45 very fine saw-like teeth; valvifers VIII slender, rounded at inner basal margin; anal segment short, ring-like; anal style (Figs. 86 a, b) strongly enlarged, ca. $1.5 \times$ longer than wide, at ventral base distinctly swollen, dorsally convex, ventrally convex at base and medially slightly concave.

Geographical Distribution. Western Indian Ocean, East Africa: Tanzania.

Diagnosis. The genus *Antidryas* n.gen. can be recognized by the body proportions, especially by the shape and proportions of the compartments of the vertex, by the antennal proportions, by the venation of the tegmina with a comparatively large outer subapical cell, and by the shape and proportions of the hind legs, especially of the post tibial spur. These external characters are combined with a characteristic configuration of the male genitalia, and especially of the female genitalia with its enlarged and ventrobasally inflated anal style.

Remarks. The type species of *Antidryas*, *Nesodryas antiope* Fennah, differs considerably in nearly all morphological characters from Hawaiian *Nesodryas*, i.e., proportions and carination of head and thorax, proportions of the antennae with 1st segment distinctly longer than wide, venation of tegmina and hind wings, spine arrangement of the hind legs and the shape of the post tibial spur, and especially in the configuration of the male genitalia. The similarity of the female genitalia with an enlarged anal style is apparently due to convergent evolution, the more as the anal style differs in details from that of the Hawaiian *Nesodryas*. As no convincing character can be assessed as synapomorphic for

both *N. antiope* and the Hawaiian *Nesodryas*, the Mascarene species apparently represents a quite different evolutionary line and thus cannot remain in *Nesodryas*. For similar morphological reasons, a close affinity to *Marquedryas* can equally not be assessed. Remarkably, the male genitalia of *N. antiope* very much resemble the configuration in the genus *Opiconsiva* Distant with the type species *Opiconsiva fuscovaria* Distant from the Seychelles Islands. However, the body proportions, the shape of the head, thorax, tegmina including venation, post tibial spur largely disagree with the current generic concept of *Opiconsiva*. It is conceivable that either the similar display of the male genital structures is due to convergent evolution, or that both taxa originated from the same stock of ancestral taxa, and subsequently diverged to different evolutionary lines.

Nesodryas antiope can no longer be regarded as a member of *Nesodryas*, and can also not be integrated into *Opiconsiva* or any other genus of the tribe Delphacini; thus, the establishment of a new genus to accommodate this unique species is warranted.

***Antidryas antiope* (Fennah), new combination (Figs. 69–85)**

Nesodryas antiope Fennah, 1964: 134.

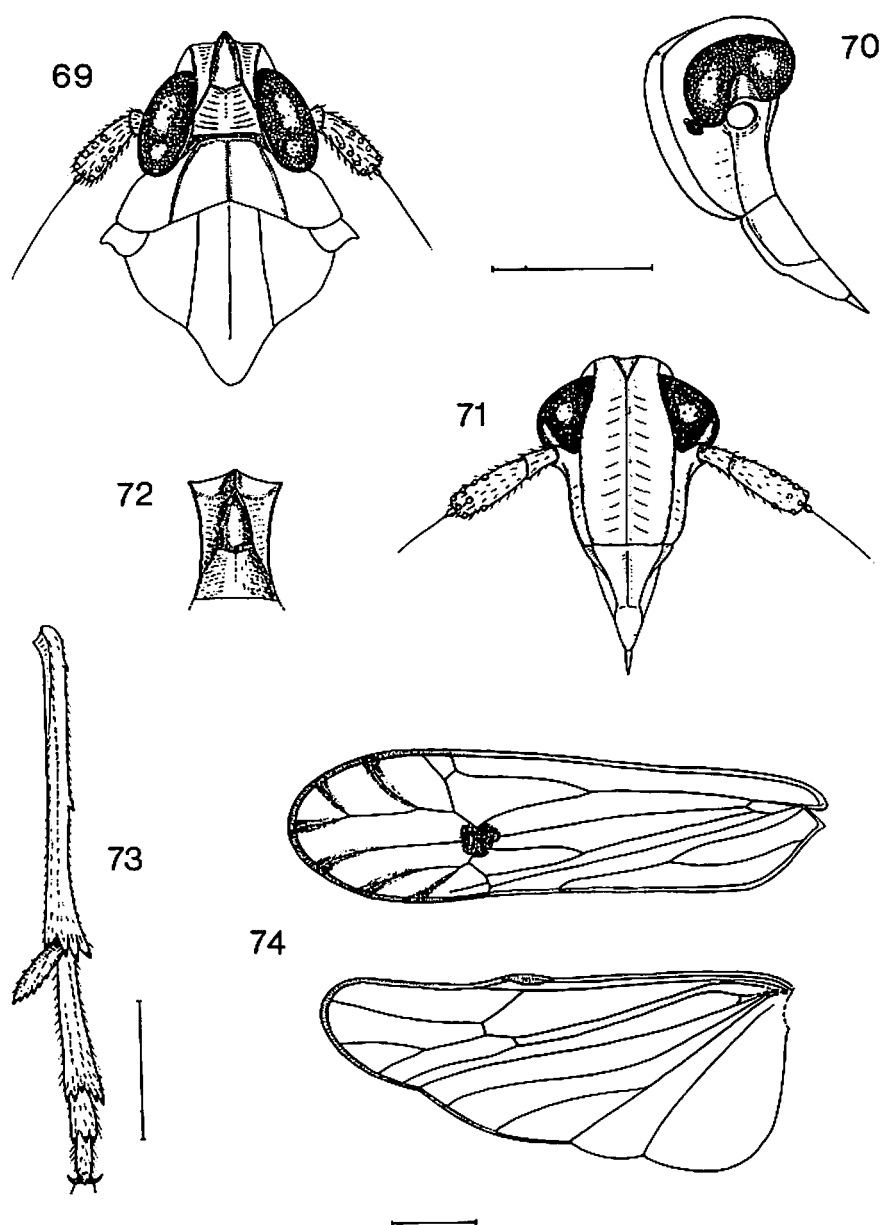
Nesodryas antiope seychellensis Fennah, 1964: 136. New synonymy.

Supplementary description. Body shape and proportions as in Fennah (1964) and in generic description. Body length (from apex of vertex to tip of tegmina): male 3.1–3.4 (3.25 mm \pm 0.09; n = 40); female 3.5–3.6 mm (3.56 \pm 0.05; n = 20). Coloration: generally as in generic description, frons and clypeus in some individuals whitish; tegmina translucent, yellowish, usually slightly powdered with wax, veins concolorous, veins in apex at margin suffusely brown; in the center of the nodal line at level of M a distinct brown spot.

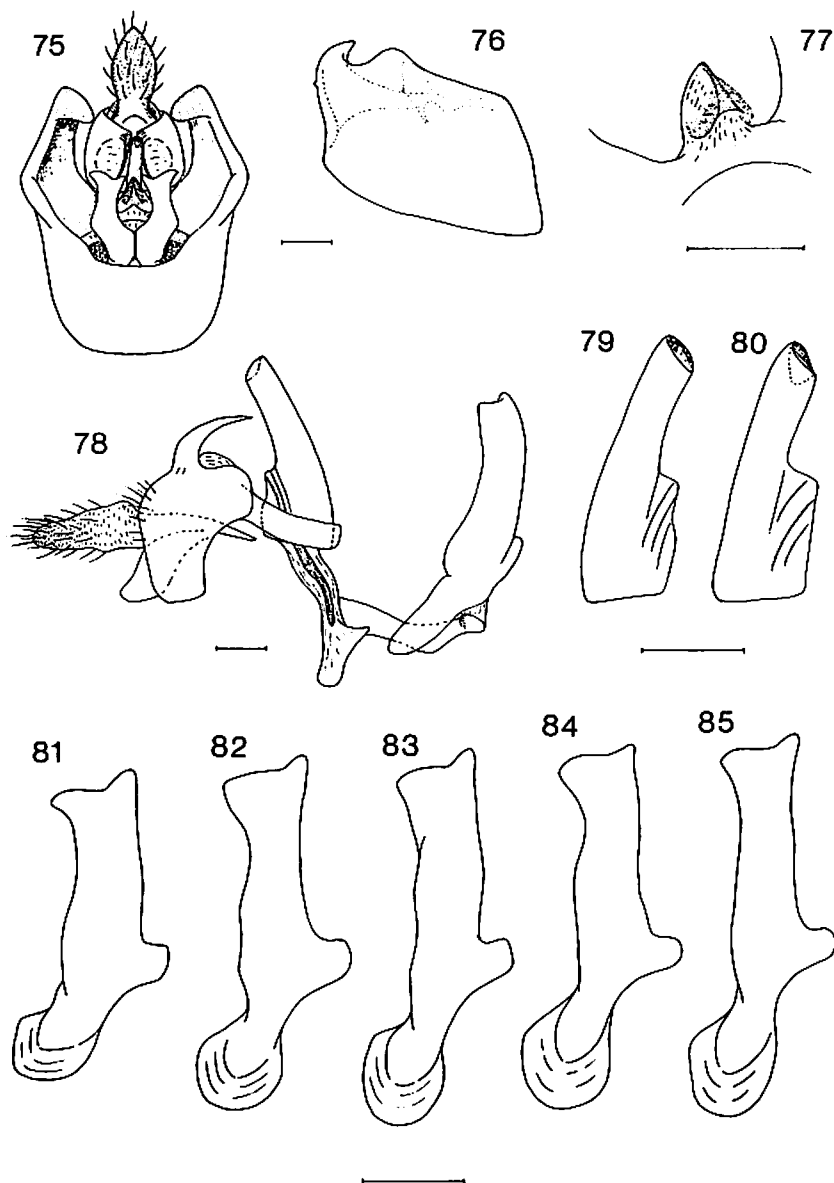
Male genitalia. Figs. 75–85. Genital segment (Figs. 75–77) with shape and proportions as in generic description; laterocaudal margins at middle angulately produced laterad; dorsocaudal corners lobe-like, projected and inflated medioventrad; median process of diaphragm (Fig. 77) steeply tectiform, medially ridged, with very fine granules. Anal segment (Figs. 75, 78) with paired spinose processes moderately long, approximate at base, then slightly diverging, in lateral aspect curved ventrad. Parameres (Figs. 75, 78, 81–85) generally as in generic description; intraspecific variation is found in shape of apex (Figs. 81–85). Aedeagus (Figs. 78–80) as in generic description; compressed basodorsal extension of shaft individually varying in size between 1/3 and 1/2 of total length of shaft, with 3–4 oblique furrows.

Female genitalia. Figs. 86–87. As in generic description.

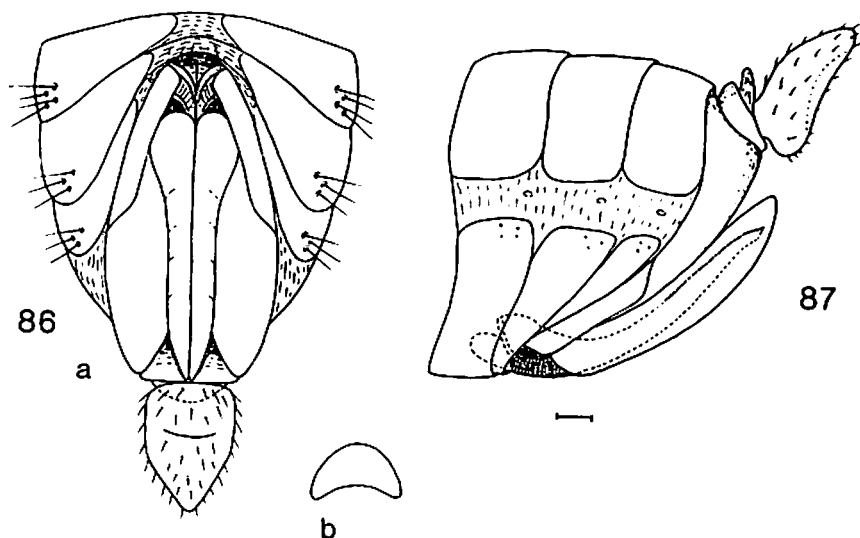
Diagnosis. *Antidryas antiope* can readily be distinguished by the slender, gracile appearance with light coloration and a conspicuous brown spot in the central nodal area of the tegmina, by the slender and solid post tibial spur with cone-shaped teeth, and by the structures of the male and female genitalia: genital segment with laterocaudal margins angulately produced laterad, dorsocaudal margins lobe-like produced and inflected medioventrad, diaphragm with a ridged, roof-like projection, configuration of anal segment and parameres as well as the short and tubular aedeagus with its basodorsal extension; anal style enlarged with ventral base swollen.



Figs. 69–74. *Antidryas antiope* (Fennah), paratype from Mauritius. 69–72, head; 69, dorsal view with pro- and mesonotum; 70, left lateral view; 71, frontal view; 72, transition of vertex to frons; 73, left hind leg with post tibial spur, underside; 74, left tegmen and hind wing. Scales: 0.5 mm.



Figs. 75-85. *Antidryas antiope* (Fennah), male genitalia. 75-79, specimen from Tanzania: Zanzibar I.; 75, genitalia in repose, ventrocaudal view; 76, genital segment, left lateral view; 77, mediodorsal process of the diaphragm, left ventral view; 78, genitalia without genital segment, left lateral view; 79, aedeagus, right lateral view; 80, same, specimen from the Seychelles Is: Marianne I.; 81-85, variation of the parameres, left paramere, ventrolateral view, specimen from: 81, Tanzania: Zanzibar; 82, Seychelles Is: Marianne I.; 83, *ibid.*, another specimen; 84, Madagascar; 85, Mauritius. Scales: 0.1 mm.



Figs. 86–87. *Antidryas antiope* (Fennah), female genitalia, specimen from the Seychelles Is: Marianne I. 86 a, abdomen, ventral view; 86 b, anal style, cross-section at middle; 87, tip of abdomen with anal style, ventral view. Scale: 0.5 mm.

Material examined. Holotype 4, glued to a triangular card mount, genitalia not dissected bearing the white labels "Mauritius, J.R. Williams, Sept. 1949", "on coconut", "209", "Com. Inst. Ent. Coll. No. 11637, "Pres. by Com. Inst. Ent. BM 1950-262" and the red labels: "holotype", "*Nesodryas antiope* (handwritten) det. R.G. Fennah". Holotype in BMNH. Paratypes: 24, 32 from Mauritius, with same locality and collecting data as holotype. Paratypes in BMNH. Non-type material. 64, 42, MADAGASCAR, East coast, Faulepointe, 3.XI.1989, ex coconut palm, A. Dabek, BMNH. 14, MAURITIUS, IV.1979, ex leaves of *Cocos nucifera*, R. Brunes, BMNH. 14, RÉUNION, St. Leu, 19.II.1976, on *Cocos nucifera*, J. Etienne, BMNH. 454, 252, SEYCHELLES IS: COUSIN I., Malaise trap, VIII–IX.1988, A. Datema, AUW; 24, 22, MARIANNE I., ex coconuts, [no date], C.J. Lomer, BMNH. 14, 12, TANZANIA: ZANZIBAR I., III.1985, ex coconuts, M. Schuiling, BMNH.

Geographical Distribution. Madagascar (Wilson 1987); Mauritius (type-locality) (Fennah 1964); Réunion (Wilson 1987); Seychelles Is: Alphonse I. (Fennah 1964, as "*Nesodryas antiope seychellensis*"), Cousin I., Marianne I.; Tanzania (Wilson 1987).

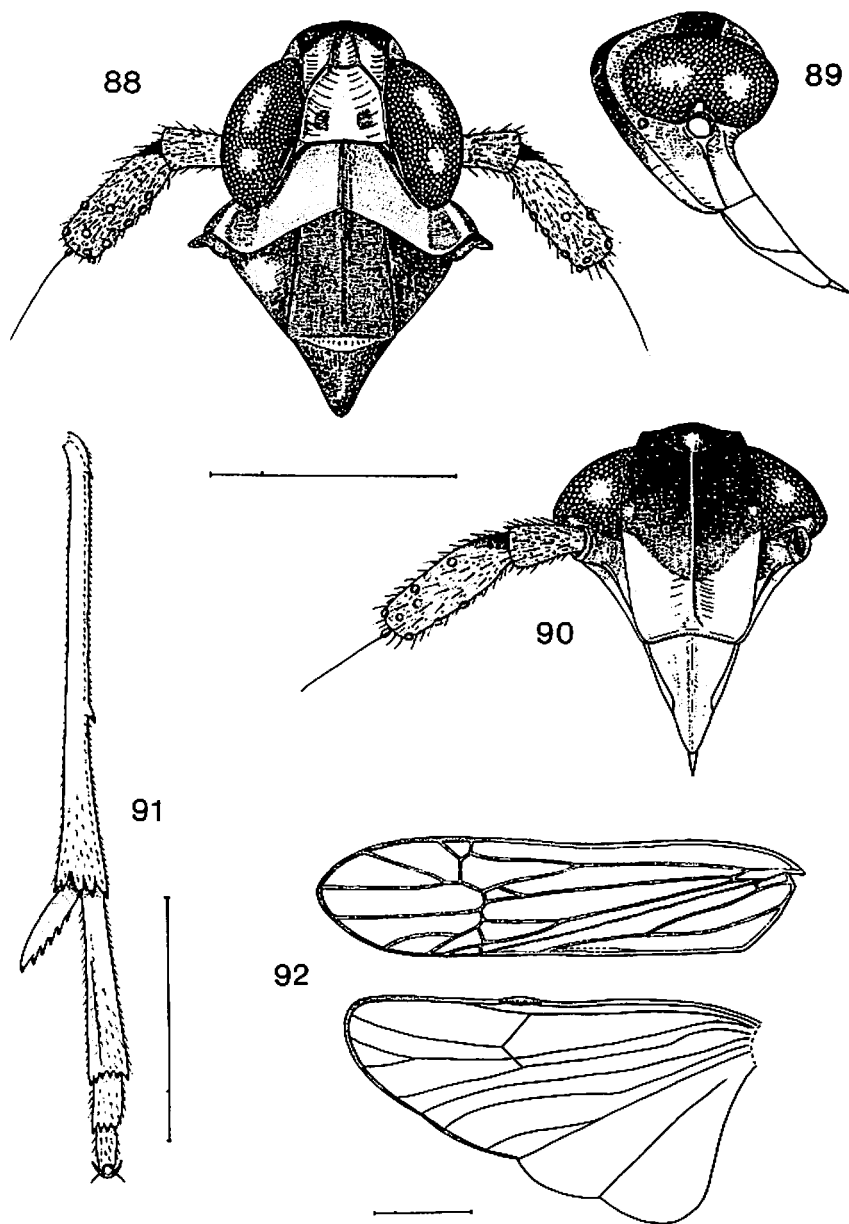
Host Plant. *Cocos nucifera* (coconut palm, Cocoideae) (Fennah 1964; Wilson 1987).

Remarks. The subspecies *Nesodryas antiope seychellensis* Fennah fits in all characters well within the morphological range of intraspecific variation of the nominate form, and is thus synonymized. *Antidryas antiope* has been reported to cause some damage, such as "hopperburn" to the leaves of coconut palms in the Seychelles Islands (see Wilson 1987). Further studies will be necessary to clarify its life history and to define its potential pest status.

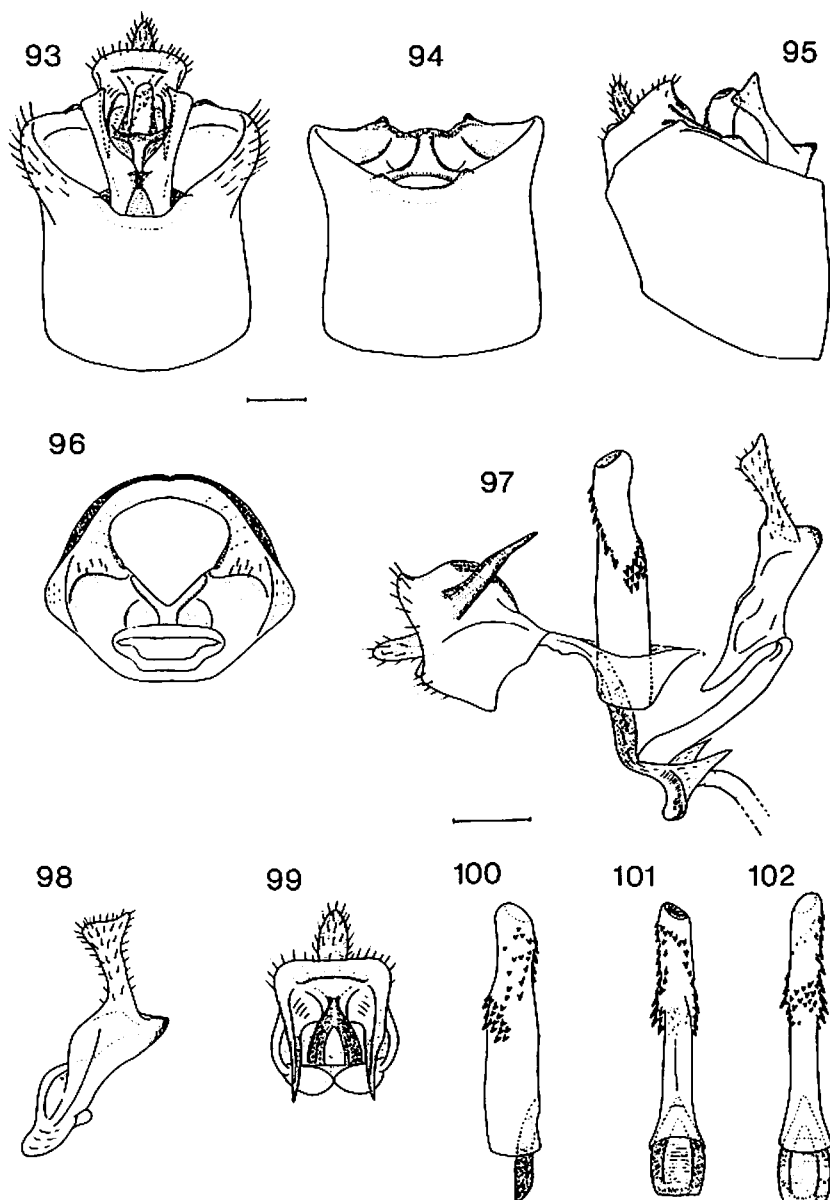
Prasliniana Asche, new genus

Type species. *Prasliniana pandanae* Asche, n.sp.; here designated.

Description. Macropterous, small, slender Delphacidae of delicate appearance. Body length including tegmina in male of type species: ca. 3 mm. Coloration: generally light colored except for thorax, vertex, and upper frons and antennal segments contrasting darker; tegmina and wings semihyaline with veins and granules concolorous; tips of spines on legs black. Head (Figs. 88–90) slightly resembling the configuration in the genus *Eumetopina* Breddin; including compound eyes ca. $2.7 \times$ wider than vertex at base and $0.9 \times$ narrower than pronotum. Vertex (Fig. 88) subrectangular, anteriorly broadly rounding onto frons, in midline ca. $1.3 \times$ longer than wide at base, lateral margins slightly concave, widening to frons; posterior compartments ca. $2.2 \times$ longer than anterior one; middle carina of posterior compartments very faint, area shallowly concave; angle between vertex and frons about 70° . Frons (Fig. 90) ca. $1.5 \times$ higher than wide (widest slightly above level of ocelli), ca. $1.8 \times$ higher than post and anteclypeus together, lateral margins slightly convex, especially lower part of frons foliately ridged; median carina simple, elevated, obsolete to vertex, frontal area gently ascending to median carina, almost plain; postclypeus with lateral carinae ridged, median carina fine but distinct; anteclypeus conical with very fine median carina. Genae (Fig. 89) with distinctly ridged oblique carina from edge of frontoclypeal suture to lower base of antennae. Ocelli distinct; compound eyes large, flat, kidney-shaped. Antennal segments (Figs. 88, 90) comparatively large, elongate, subcylindrical, slightly compressed, 1st segment ca. $1.9 \times$ longer than wide, 2nd segment ca. $3 \times$ longer than wide and ca. $1.85 \times$ longer than 1st; ca. 15–16 sensory fields distributed on each 2nd antennal segment, in the type species following a pattern that is slightly aberrant from the usual 16-7 pattern (see Figs. 88, 90). Rostrum attaining anterior margin of post trochanters. Pronotum (Fig. 88) in midline ca. $0.56 \times$ shorter than vertex; posterior margin flat, angulately excavated; median carina distinct, reaching posterior margin; lateral carinae faint, curved around posterior margins of compound eyes, not attaining posterior margin of pronotum; mesonotum (Fig. 88) in midline ca. $3 \times$ longer than pronotum; lateral carinae straight, attaining posterior margin; dorsal disc slightly inflected. Tegmina (Fig. 92) steeply tectiformous, long and narrow, in type species surpassing tip of abdomen by ca. $1/2$ their length, slightly tapering to apex, subapical cells relatively small; commissural margin in claval area very narrowly foliately elevated; entry of claval vein into commissural margin in an acute angle; veins with fine granules; hindwings (Fig. 92) with Cu and M close and parallel to each other. Legs slender; post tibia (Fig. 91) ca. $1.6 \times$ longer than post tarsi, laterally with 2, distally with 5 (2+3) spines; 1st post tarsus (Fig. 91) ca. $2.2 \times$ longer than 2nd and 3rd post tarsi segment together; 1st post tarsus distally with 6 (2+4) spines, 2nd post tarsus distally with 4 spines in a row; post tibial spur (Fig. 91) sub-



Figs. 88-92. *Prasiniana pandanae* Asche, n.gen., n.sp., holotype from the Seychelles Is: Praslin I. 88-90, head; 88, dorsal view with pro- and mesonotum; 89, left lateral view; 90, frontal view; 91, left hind leg with post tibial spur, underside; 92, left tegmen and hind wing. Scales: 0.5 mm.



Figs. 93–102. *Prasliniana pandanae* Asche, n.gen., n.sp., male genitalia, holotype from the Seychelles Is: *Praslin* I. 93, genitalia in repose, ventrocaudal view; 94, genital segment, ventral view; 95, genitalia in repose, left lateral view; 96, genital segment, caudal view; 97, genitalia without genital segment, left lateral view; 98, left paramere, ventrolateral view; 99, anal segment, ventral view; 100, aedeagus, right lateral view; 101, same, dorsal view; 102, same, ventral view. Scales: 0.1 mm.

ulate with distinct terminal tooth, in type species inner margin with 5 well separated cone-shaped teeth. Male drumming organ with well developed central plate in 2nd abdominal tergite, with comparatively sturdy and short paired apodemes of 2nd abdominal sternite, erected dorsad but not reaching tergites.

Male genitalia. Figs. 93–102. Genital segment (Figs. 93–96) in caudal aspect flat, ovate, in lateral aspect irregularly pentangular, lateral margins produced laterocaudad, rounded, dorsocaudal edges slightly produced, ventrally ca. $3.8 \times$ higher than dorsally, ventrocaudal margin shallowly concave; diaphragm with dorsal margin deeply excavated, medially ridged, opening for parameres flat, mushroom-shaped. Anal segment (Figs. 97, 99) short, ring-like, ventrocaudally closed by sclerotized bridge, ventral side partly membranous, partly sclerotized, a spinose, apically pointed process directed ventrad arising from each side; anal style moderately long. Parameres (Figs. 93, 97, 98) with ventrobasal margin cone-shaped produced mediad, tip slightly dilated, apically truncate. Aedeagus (Figs. 97, 100–102) tubular, slightly compressed, straight, phallotreme apically, with numerous teeth in apical 1/2; suspensorium short, forming calyptra around aedeagal base; connective moderately long, nearly straight.

Females. Unknown.

Diagnosis. *Prasliniana* n.gen. can be distinguished by the following combination of characters: very small body size, relatively flat vertex with posterior compartments very large, anteriorly rounding onto frons, angle vertex to frons ca. 70° ; frons with lateral margins laminate; antennal segments enlarged with irregular pattern of sensory fields; lateral carinae of pronotum not reaching the posterior margin, curved behind the eyes; tegmina very long, slender, steeply tectiform; legs long, slender, post tibial spur subulate with about 5 conical teeth; genital segment with laterocaudal margin produced laterad, anal segment with sclerotized elements within the otherwise membranous ventral side, and with distinctly laterally originating paired spinose processes, and tubular aedeagus with apical phallotreme and numerous teeth in apical half. It differs from *Antidryas* n.gen. and from the second "alohine" genus from the Seychelles, *Ambarvalia* Distant (see Distant 1917; Fennah 1964; Asche 1985), by the body proportions, coloration, carination of vertex and pronotum, and by the shape of the genital structures.

Geographical Distribution. Seychelles Is.

Remarks. The following characters are interpreted as apomorphic and characterize the genus: the configuration of the head with enlarged and fairly robust antennae, the pronotal carination, the shape of the genital segment, the unique configuration of the anal segment, and the aedeagus with its ornamentation by numerous teeth in the distal half of its shaft. Within the Delphacini, *Prasliniana* n.gen. appears to be rather isolated. By the unique display of characters, it differs considerably not only from the other "alohine" genera of the Mascarene Islands, Madagascar, and East Africa (*Ambarvalia*, *Antidryas*), but also from the West African genus *Afrosydne* Fennah (see Fennah 1969), and the South Atlantic genus *Ilburnia* White (see e.g., Fennah 1976). Equally, I can currently see no indication for close relationships of *Prasliniana* to any of the "alohine" genera of the Pacific Region.

Prasliniana pandanae Asche, new species (Figs. 88–102)

Description. Body length of male: from apex of vertex to tip of abdomen 1.9 mm, from apex of vertex to tip of tegmina 3.0 mm. Coloration: ground color pale stramineous to light brown, legs whitish to pale yellow; vertex shiny light yellow-brown with margins darker, a diffusely dark brown mark in each posterior compartment; transition to frons and upper frons dark golden brown, lower frons, post and anteclypeus whitish to pale yellow, lateral parts of head light brown except for whitish parts above and below frontoclypeal suture, small dark brown band between upper margin of compound eyes and lateral margin of vertex; ocelli dark brown, compound eyes red; antennal segments medium to dark brown, darker mark at anterior base of 2nd segment. Pronotum light yellow-brown, mesonotum and tegulae medium to chestnut brown. Tegmina and wings yellowish, veins and granules concolorous. Male genitalia honey yellow. Shape and proportions of head, thorax, antennal segments, and legs including post tibial spur, as in generic description. Tegmina ca. $4.75 \times$ longer than wide (widest shortly distad of nodal line), venation with slight irregularities of M at nodal line as in Fig. 92.; granules very faint.

Male genitalia. Figs. 93–102. Genital segment (Figs. 93–96) in caudal aspect ca. $1.23 \times$ wider than high, laterocaudal margins almost angulately produced laterad; each laterodorsal corner produced into small protuberance; median excavation of ventrocaudal margin shallowly concave, on each side flanked by short lobe; diaphragm (Fig. 96) with dorsal margin deeply V-shaped, centrally elevated, forming Y-shaped, rounded ridge, portions laterad of ridge concave. Anal segment (Figs. 97, 99) ventrocaudally slightly produced, ventral surface vaulted, mostly membranous but medially with an inversely Y-shaped sclerite; paired spinose processes moderately long, in middle slightly bent ventrad. Parameres (Figs. 93, 97, 98) with broad base, cone-shaped process on ventral margin robust, middle part building short, slender stem, apically inverse triangularly dilated, spatulate, apex truncate, inner edge pointed, produced mediad. Aedeagus (Figs. 97, 100–102) relatively short, straight, subapically slightly narrowed, phallotreme apically and slightly exposed to dorsocaudal side, numerous small teeth in upper 1/2 of shaft on all sides, partly forming rows, partly clusters.

Females. Unknown.

Type data. Holotype 4, SEYCHELLES IS: PRASLIN I., Vallée de Mai, sur *Pandanus hornei*, 25.VII.1972, P.L.G. Benoit & J.J. Van Mol, Miss. Zool. belge aux Séchelles. Holotype in MRAC.

Geographical Distribution. Seychelles Is.: Praslin I.

Host Plant. *Pandanus hornei* (Pandanaceae).

DISCUSSION

The present work may raise the general question of the use of “splitting” genera that have seemingly been of practical value for a long time. Fennah (1958) refused to recognize “alohine” genera other than the Hawaiian ones for the southeast Polynesian delphacids, because he believed that “true fundamental relationships” would be obscured by establishing small Polynesian species groups as separate genera. Accordingly, he placed the genus *Nesodryas* within rather broad limits based mainly on the characters used by Zimmerman in his key for the Hawaiian genera (Zimmerman 1948: 139). For the south-

eastern Polynesian species, Fennah (1958: 159, key) defined *Nesodryas* clearly as a taxon with the "1st antennal segment not distinctly longer than broad". However, a few pages further for *Nesodryas oenone*, Fennah indicated the proportions of the 1st antennal segment as "basal segment distinctly longer than broad (1.8:1)". The same inconsistency in Fennah's generic interpretation of *Nesodryas* applies to *Nesodryas antiope* (see Fennah 1964), which again displays quite different antennal proportions than the type species from Hawaii. This demonstrates how unsatisfying Fennah's definition of *Nesodryas* was, even for practical use. In modern systematics, a genus is generally regarded as a unit that includes a species or a group of phylogenetically related species, i.e., a genus should be assessed as a monophyletic unit which can only be based on apomorphic characters. None of the "alohine" genera has been analyzed phylogenetically. They still represent phenetic units that were established for mere diagnostic purpose (and mostly insufficiently even in this regard).

The present study has revealed substantial morphological differences between the species placed in *Nesodryas* from Hawaii, the Marquesas, and the Indian Ocean both in body proportions and genital characters of the male and female genitalia. Not a single character could be found that is apt to be interpreted as a synapomorphy for these taxa, thus close relationships between them cannot be assessed. Conversely, the heterogeneous morphological display strongly supports the assumption that the 3 geographically well separated taxa represent quite different evolutionary lines. Therefore, *Nesodryas* sensu Fennah must be regarded as polyphyletic. In contrast to Fennah (1958), I believe that persisting in this situation would really mean to obscure "true fundamental relationships" and inevitably lead to mistaken zoogeographical conclusions. The division of *Nesodryas* into 3 separate, monophyletic genera is therefore the logical consequence: *Nesodryas* s.str. is now with 2 species endemic in the Hawaiian Islands, *Marquedryas* with 3 species endemic in the Marquesas Islands, and *Antidryas* with 1 species confined to the southwestern Indian Ocean islands and southeastern Africa. As these taxa are not closely related, they may have derived from different, yet unknown sources. Fennah's assumption of a Pre-Glacial Antarctic continent as a potential source for "alohine" delphacids (Fennah 1964) should be reconsidered with the background of polyphyly of this group. Currently, neither Antarctica, nor any other geographical regions can be favored for the origin of *Nesodryas* and other "alohine" taxa.

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